UNIVERSIDAD DA CORUÑA
Departamento de Bioloxía Animal, B. Vexetal e Ecoloxía

Tesis doctoral

EFECTO DEL EVENTO EL NIÑO SOBRE LA ESTRUCTURA DE LA COMUNIDAD DE LARVAS DE PECES Y BIOMASA ZOOPLÁNCTICA EN EL PACÍFICO CENTRAL MEXICANO

María del Carmen Franco-Gordo

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A Coruña, España.
Febrero 2004

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CERTIFICA:

Que la presente tesis titulada " Efecto del evento El Niño sobre la estructura de la comunidad de larvas de peces y biomasa zooplánctica en el Pacífico central Mexicano", presentada por María del Carmen Franco Gordo fue realizada bajo mi dirección y considero reúne todas las condiciones para aspirar al grado de doctor.

Para que conste, firmo la presente certificación en A Coruña a 24 de enero de 2004.

Fdo. Juan Freire Botana

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Capítulo 1

Introducción General

Introducción General

Los patrones espaciales y temporales de la distribución del zooplancton y las larvas de peces están determinados por la interacción de múltiples procesos bióticos y abióticos. Como factores biológicos se incluyen la localización, tiempo y modo de desove de adultos, duración del ciclo larval, comportamiento larval, tasa de depredación, alimentación y crecimiento (Leis 1991), mientras que los factores físicos incluyen eventos hidrológicos como corrientes, vientos, remolinos, afloramientos y estratificación de la columna de agua (Haury et al. 1978; Owen 1981; Denman y Powell 1984; Norcross y Shaw 1984; Kingsford 1990). Una gran variedad de procesos oceanográficos influye en los patrones de transporte larval (Norcross y Shaw 1984; Werner et al. 1997). Las larvas de peces de aguas costeras están fuertemente influenciadas por procesos a meso-escala, como la distancia a la costa (Leis, 1982), proximidad a arrecifes (Kingsford y Choat 1989), eddies (Hare y Cowen 1996) y eventos de afloramiento o surgencias (Olivar 1990). En escalas mayores, debido al fenómeno El Niño, la alteración de las corrientes marinas puede influenciar la dispersión larval (Cowen 1985; Pearce y Phillips 1988) y por ende la distribución del ictioplancton.

El Pacífico oriental es una región con una variabilidad oceanográfica interanual asociada con El Niño Oscilación del Sur (ENSO). Los episodios ENSO causan grandes alteraciones en todo el océano Pacífico principalmente por el desplazamiento de agua caliente, el hundimiento de la nutriclina y la reducción de la producción de fitoplancton. La estructura de la temperatura superficial del mar cambia sustancialmente en espacio y tiempo, dando como resultado cambios en la presión atmosférica, en el patrón de corrientes marinas y en el nivel del mar (Chávez et al 1999; 2000).

Los efectos biológicos del ENSO han sido menos documentados que sus efectos físicos, la mayor información se concentra en El Niño 1982-1983 y 1997-1998 en el sistema de la Corriente de California (CCS). En estos eventos, se produjo una reducción de producción primaria en las áreas de afloramiento (Fiedler 1984; 2002; Bogrard y Lynn 2001; Chávez et al. 2002) aparentemente debido al bajo aporte de nutrientes. La biomasa de zooplancton también disminuyó (Chelton et al. 1982; McGowan 1985; Chávez et al. 2002), probablemente debido a la carencia en el suministro de alimento. La insuficiencia de plancton produce una reacción en cadena en los niveles tróficos superiores, pero el decremento en biomasas no necesariamente induce a similares efectos entre taxa; las poblaciones tropicales y subtropicales pueden ser más abundantes que lo habitual y las poblaciones subárticas decrecen notablemente durante los eventos ENSO. En la Corriente de Humboldt se remplazó la anchoveta por la sardina y fue atribuido a la baja disponibilidad de

fitoplancton que es utilizado como fuente de alimento por la anchoveta, y a la actividad depredatoria de la sardina sobre los huevos de anchoveta (Arntz y Fahrbach 1996). El modelo de recomposición y tropicalización de las especies durante los eventos El Niño aparentemente funciona en zonas subárticas, templadas y subtropicales del Pacifico oriental, sin embargo en las zonas tropicales se desconocen los efectos debido principalmente a la escasez de estudios.

1.1 Antecedentes

Las investigaciones del ictioplancton y de la biomasa zooplánctica se inician en el Pacifico Nororiental en el área de la Corriente de California, impulsadas principalmente por el programa CalCOFI (California Cooperative Oceanic Fisheries Investigations) en el año de 1949 como respuesta al colapso de la pesquería de sardina del Pacífico *Sardinops sagax*. Desde entonces se han generado múltiples trabajos enfocados hacia diversos aspectos del zooplancton y de larvas de peces. Una de las últimas aportaciones del programa CalCOFI sobre larvas de peces es el de Moser (1996) basado en la colección de ictioplancton acumulada desde 1951 hasta 1994 en un área comprendida desde el norte de California hasta Cabo San Lucas Baja California Sur incluyendo el golfo de California en el que se detallan más de 550 especies de larvas de peces mencionando su hábitat, distribución geográfica, y el tipo de huevo y larva. Este

trabajo ha sido básico en la identificación de los especimenes de esta tesis.

Las investigaciones específicas de larvas de peces en el Pacífico tropical oriental se inician con los cruceros EASTROPAC en 1972 y destacan por la amplitud de área de muestreo (20°N - 20°S), sin embargo estos cruceros no fueron secuenciales y solo describen la composición y abundancia de larvas en determinadas épocas del año. En el Pacífico mexicano existen muy pocos estudios que evalúan el efecto de El Niño y La Niña en las comunidades de zooplancton

1.2 Variabilidad hidroclimática en el Pacifico central mexicano

En la costa oriental mexicana (12°N - 32°N) dominan dos corrientes marinas superficiales: La corriente de California (CC) y la Contracorriente Norecuatorial (CCNE). La CC es muy ancha (mayor de 800 km), con una profundidad de aproximadamente 500 m, velocidades típicas de 20 cm/ segundo y con un movimiento de norte a sur paralelo a las costas orientales de Canadá, Estados Unidos de América y México. Esta corriente se caracteriza por aguas frías de baja salinidad (34.5 psu) (Zamudio et al. 2001; Aguirre-Gómez, et al. 2003). La CC domina la circulación de la península de Baja California durante todo el año. A finales de invierno y principios de primavera la corriente es más fuerte y penetra hasta los de 15 ° latitud (Zamudio, et al. 2001). La CCNE tiene influencia en las costas surorientales

mexicanas, se caracteriza por su agua cálida y salinidad intermedia (34.6-34.85) con flujo hacia el norte desde los 5° a 23°N desde mediados de primavera hasta finales de otoño. Esta corriente juega un papel muy importante en el transporte de aguas sub-superficiales, subtropicales hacia latitudes del norte (Badan, et al. 1989; 1997; Filonov, et al. 2000).

La zona donde la CC y CCNE se juntan es conocida como zona de transición y geográficamente su posición es variable (Wyrtki 1965) ya que depende de la intensidad relativa de estas corrientes y principalmente de la prevalencia de los vientos superficiales en la región nororiental. Durante el invierno, cuando la CC es más intensa, la zona de transición esta localizada más hacia el sur, mientras que en el verano cuando la Contracorriente es fuerte, la zona de transición se mueve hacia el norte.

1.3 El Niño Oscilación del Sur (ENSO)

El Niño Oscilación del Sur (ENSO) es una fluctuación irregular que involucra a todo el océano del Pacífico tropical y de una manera global a la atmósfera (Philander 1999). El ENSO consiste en una interacción inestable entre la temperatura superficial del mar (SST) y la presión atmosférica; el resultado es una serie de variaciones en los vientos, las precipitaciones, la profundidad de la termoclina, la circulación oceánica y cambios en la productividad biológica y en la alimentación y reproducción de peces, aves y mamíferos (Fiedler

2002). En la actualidad el término ENSO se ha definido como el ciclo completo de eventos cálidos y eventos fríos en el océano Pacífico ecuatorial, de tal forma que El Niño es el componente oceánico y la Oscilación del Sur el componente atmosférico, por consiguiente las siglas ENSO El Niño/Southern Oscillation es un ciclo irregular en duración e intensidad, cada evento puede durar cerca de un año, pero asociado a anomalías climáticas que pueden persistir mucho mas tiempo en algunas partes del mundo. También varía en dimensionalidad tanto para calentamientos extremos (El Niño) como para enfriamientos (La Niña). Philander (1990) propuso el término La Niña para complementar la fase fría. Durante La Niña las regiones cálidas con abundantes precipitaciones y baja presión superficial son confinadas lejos del Pacífico tropical occidental (Philander 1998).

1.4 Condiciones del evento ENSO

En condiciones normales, los vientos alisios del este mantienen un equilibrio entre las aguas calientes del Pacífico occidental y las aguas frías del Pacífico oriental. La radiación solar calienta el agua del este, y la termoclina (y nutriclina) se encuentra a 40 o 50 m bajo la superficie en el Pacífico oriental, los vientos y afloramientos son fuertes en el Pacífico central (Philander 1998; 1999; Chávez et al. 1999). Mientras que en el Pacífico occidental se acumula agua caliente y se forman nubes tormentosas por encima de estas aguas cálidas (figura 1). Cuando existe un calentamiento anómalo (El Niño), los vientos alisios del este se debilitan, el agua cálida del Pacífico

occidental fluye hacia el este; esta capa de unos 150 m de profundidad, fluye sobre aguas más frías ricas en nutrientes y bloquea su ascenso a lo largo de todo su trayecto. El aire obtiene calor y humedad de la superficie cálida del océano y se eleva formando nubes de tormenta en el Pacífico central (Bograd y Lynn 2001).

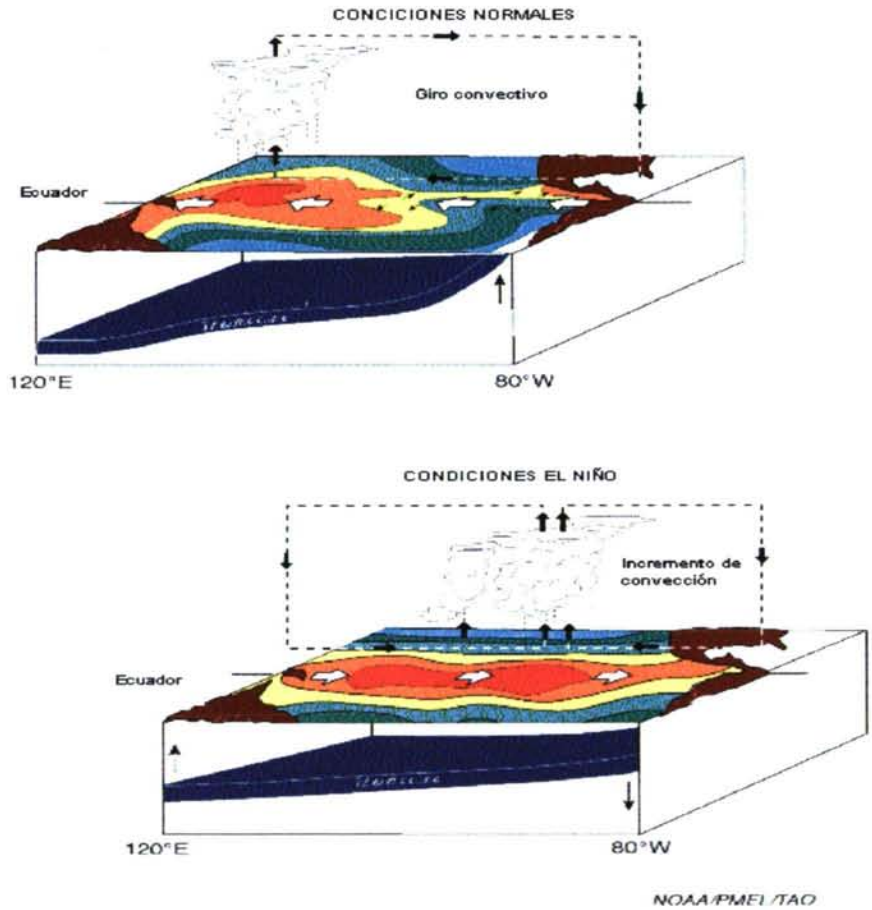

Figura 1. Condiciones océano-atmosféricas normales (arriba) y en un evento de El Niño (abajo). Imágenes tomadas http://ivanova.gsfc.nasa.gov.

1.5 Evolución de El Niño 1997-1998

El Niño 1997-1998 ha sido el evento más fuerte en los últimos 200 años (McPhaden 1999; Kerr 1998). Desde marzo de 1997, el Pacífico tropical experimentó patrones anómalos de lluvias, abundancia de nubes y presión atmosférica. Los vientos fueron casi interrumpidos a lo largo del Ecuador y la actividad ciclónica del Pacífico nororiental se incrementó (CPC, 1997). El Niño 97-98 fue extremadamente severo y tuvo una fuerte anomalía de temperatura superficial del mar (>2.0 ºC) que se extendió desde aproximadamente 160 E a 80 W, según los datos del Nasa Scatterometer (NSCAT) se inició en abril-mayo de 1997 y sus efectos se extendieron hasta principios del verano de 1998.

A escala mundial se observaron inviernos severos e incendios forestales en América Central, Indonesia, Australia y el sureste de África así como fuertes lluvias en Ecuador y Perú. Estos cambios en las condiciones atmosféricas fueron debidos a las modificaciones en la temperatura superficial del mar del Pacífico tropical, especialmente la expansión del área cubierta por aguas más cálidas que 28°C (figura 2). Durante La Niña estas aguas cubren un área relativamente mas pequeña en el Pacífico oriental tropical y durante El Niño el área se extiende hasta cubrir mucho mas allá de Ecuador y Perú (Philander 1998). Las condiciones durante 1997-1998 fueron similares a los que se observan en giros oligotróficos (Chávez y

Toggweiler, 1995), con un hundimiento de nitratos a mas de 100 m de profundidad y una disminución de la producción primaria.

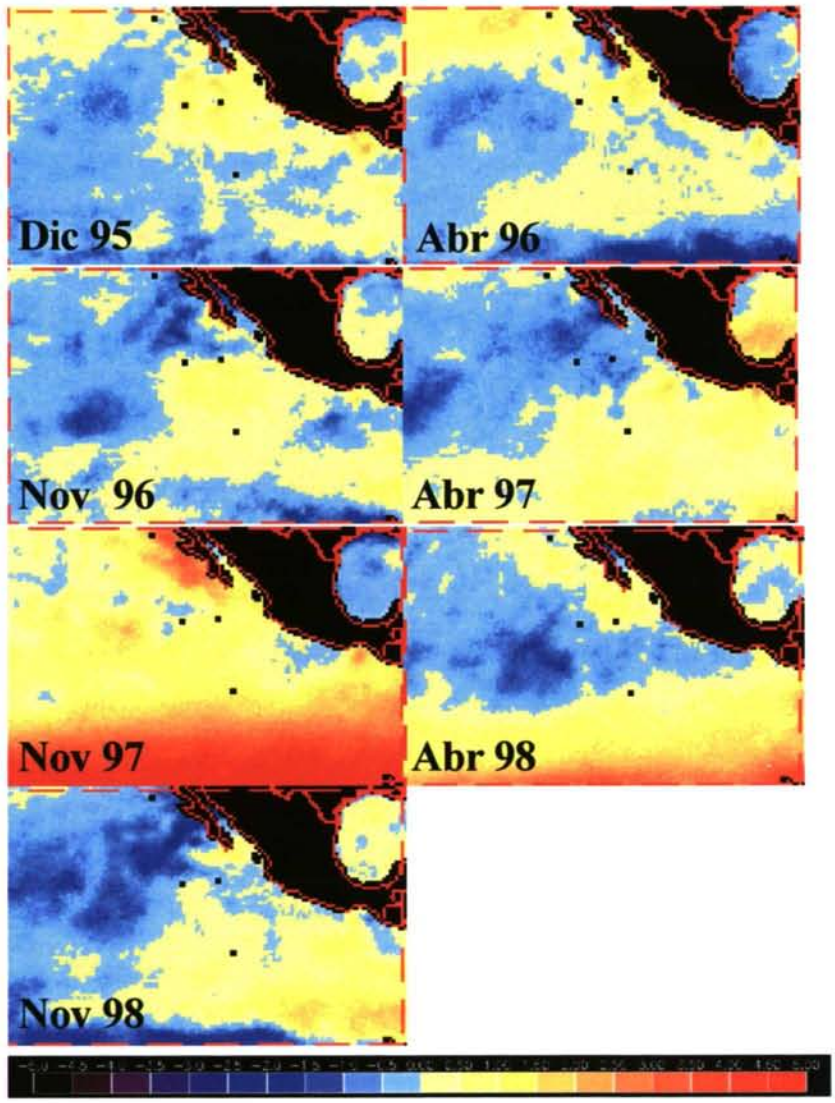

Figura 2. Anomalías de la temperatura superficial del mar en el Pacífico Tropical oriental durante periodo de estudio. Información de imágenes de satélite tomada de la National Oceanic and Atmospheric Administration NOAA.

1.6 Consecuencias biológicas en el Pacífico oriental del ENSO

La rápida transición de El Niño a condiciones La Niña en el Pacífico ecuatorial en 1998 fue acompañada por considerables variaciones ambientales en el sistema de la Corriente de California (CCS). En regiones costeras El Niño se caracterizó por una elevación del nivel del mar y el hundimiento de la nutriclina. Existieron perturbaciones químicas y biológicas asociadas con este evento, la más notable fue una fuerte reducción de los afloramientos cerca del Ecuador y los más bajos registros de concentraciones de clorofilas (Chávez et al. 1998; 1999). Por el contrario las condiciones de La Niña dieron lugar a una notable recuperación de la producción biológica en los últimos meses de 1998, y la reanudación del ciclo de vientos incrementaron los afloramientos dando como resultado el más extenso "bloom" de fitoplancton observado el Pacífico ecuatorial (Chávez et al. 1999). Los eventos biológicos que ocurren en condiciones de El Niño varían geográficamente y no pueden generalizarse ya que las condiciones ambientales influyen de manera diferencial en distintas especies y en una misma especie a lo largo de su ciclo de vida, por ejemplo en la CC se ha observado una disminución de la biomasa de zooplancton durante los eventos (Lavaniegos et al. 2002; Mackas y Galbraith 2002; Roemmich y McGowan 1995), aunque también se han reportado incrementos en la biomasa en el Pacífico subártico (Brodeur y Ware 1992; Brodeur et al. 1996).

Los cambios en la biomasa del zooplancton frecuentemente están asociados a cambios en la composición de especies; por ejemplo, la presencia de especies tropicales en el Pacífico Nororiental durante períodos El Niño sido detectada en larvas de peces (Funes-Rodríguez et al. 1995; 1998; 2003; Avalos-García et al. 2003; Sánchez-Velasco et al. 2000; Smith y Moser 2003), en copépodos (Mullin 1998; Lavaniegos et al. 2003), en eufaúsidos (Gómez-Gutiérrez et al. 1995; Mackas y Galbraith 2002; Marinovic et al. 2002; Brinton y Townsend 2003) y en tunicados (Lavaniegos y Ohman 2003). Durante El Niño 1997-1998 los arrecifes de coral presentaron blanquecimiento en el Golfo de California y en las costas orientales de México (Reyes-Bonilla 2001; Reyes-Bonilla et al. 2002) en estos mismos años las biomasas de zooplancton del norte de Chile no presentaron cambios considerables aunque incrementó la abundancia relativa de pequeños copépodos (González et al. 2000).

1.7 Hipótesis

Los patrones de distribución y abundancia del zooplancton dependen de distintos fenómenos físicos que operan en diferentes escalas espaciales, cuyos intervalos varían desde >1 a 1000 km (Haury et al. 1978; Denman y Powell 1984). Algunos de los factores físicos incluyen eventos hidrográficos como corrientes, vientos, remolinos y eddies, afloramientos y estratificación de la columna de agua (Haury et al. 1978; Owen 1981). Estas características pueden influenciar potencialmente la dispersión, supervivencia y reclutamiento de

organismos en el zooplancton. Las variaciones temporales de los procesos oceanográficos de pequeña o gran escala tienen influencia sobre los patrones de distribución y abundancia de las asociaciones plánctica (Haury et al. 1978; McGowen 1993). Sin embargo el efecto en los organismos marinos es muy complejo debido a que interactúan diferentes factores en distintas escalas de tiempo y espacio, y estas interacciones son difíciles de establecer ya que los factores ambientales influyen diferencialmente sobre las especies y en una misma especie a lo largo de su ciclo de vida.

El conocimiento acerca de los eventos El Niño y La Niña se ha incrementado en los últimos años, de tal forma que la variabilidad ambiental en el Océano Pacífico empieza a ser comprendida (Philander, 1998; Chávez et al. 1999; 2002; Fedorov y Philander 2000; Bograd y Lynn 2001; Lehodey 2001; Fiedler 2002), aunque en escalas regionales el conocimiento acerca de los impactos ecológicos en todos los hábitat marinos permanecen parcial y espacialmente fragmentados. La magnitud, e incluso la señal de repuesta difiere entre regiones, se sabe que la respuesta más inmediata se presenta en los niveles tróficos mas bajos, aunque también puede observarse en muchos otros niveles (Mullin 1995; Fulton y Le Brasseur 1985; Brodeur et al. 1992).

Por lo anterior y de acuerdo con los principios y observaciones relativos al estudio de las comunidades del zooplancton y de la

influencia que sobre ellos tienen los factores abióticos se plantean las siguientes hipótesis de trabajo:

-Durante el periodo de estudio (1995-1998) habrá una recomposición de la comunidad de larvas de peces influenciada por la presencia de aguas cálidas derivadas del evento ENSO, por cambios estacionales y por factores comportamentales (alimentación, agregación) y ontogenéticos.

-Existirán diferencias en los patrones de abundancia y distribución del zooplancton y de las larvas de peces que estarán determinadas principalmente por procesos físicos de mesoescala y su variabilidad ligada a las distintas épocas climáticas.

1.8 Objetivo

La presente tesis doctoral tiene como fin el estudio de la biomasa zooplánctica y las larvas de peces recolectadas en la plataforma continental de las costas de Jalisco y Colima durante 27 meses (1995-1998), el periodo incluye uno de los más fuertes eventos océano-atmosféricos en los últimos 200 años: El Niño 1997-1998. El objetivo final es conocer la dinámica temporal y espacial de la biomasa zooplánctica y de las asociaciones de larvas de peces y determinar el efecto de las diferentes fuentes de variabilidad: estacional, interanual en los patrones espaciales de distribución. Se plantea que la estacionalidad (pautas hidroclimáticas) y el fenómeno El Niño son los principales factores que determinan la variación

espacio-temporal de los organismos plánctcos, de las asociaciones de larvas de peces y su diversidad. Se asume que la característica principal de los patrones de distribución espacial está determinada por la distancia a la costa. Los métodos de evaluación utilizados en este estudio ayudarán a discernir las dependencias ecológicas entre las biomasas de zooplancton, las larvas de peces y los factores físicos, indicando su variabilidad en espacio y tiempo, aspectos que serán descritos objetivamente con métodos estadísticos.

1.8.1 Objetivos específicos

1. Determinar los patrones espacio-temporales de la biomasa plánctica y describir los factores más influyentes en la distribución del zooplancton marino en las costas de Jalisco y Colima, México.

    1.1 Determinar las pautas de estacionalidad en la producción zooplánctica y fitoplánctica, así como su relación con los procesos costeros.

    1.2 Determinar los patrones de variabilidad de la biomasa plánctica en relación con la distancia de la costa y profundidad y los procesos costeros.

2. Establecer la composición, distribución y abundancia del ictioplancton en la costa de Jalisco y Colima y determinar las principales pautas de su distribución en el tiempo y el espacio

2.1 Analizar la relación que guardan las pautas de variabilidad de la abundancia ictioplánctica con las condiciones hidrológicas locales y los patrones de producción primaria y secundaria.

2.2 Determinar la influencia que los procesos costeros y en particular los mecanismos de transporte y la disponibilidad de nutrientes en los patrones de distribución espacial del ictioplancton.

3. Determinar la variabilidad espacial y temporal de las asociaciones de larvas de peces y explorar los patrones dependientes de escala que determinan la organización de la comunidad.

3.1 Determinar y tipificar las asociaciones de especies para las diferentes pautas hidroclimáticas de variación intraanual y su segregación espacial.

3.2 Determinar la diversidad del ictioplancton y sus patrones espacio-temporales y establecer factores ambientales relacionados con la riqueza de específica, equitatividad y diversidad de especies.

4. Describir la variabilidad hidrográfica durante el evento El Niño 1997-1998 en aguas costeras de los estados de Jalisco y Colima, México.

4.1 Determinar las pautas de variabilidad temporal de las principales variables físicas de la masa de agua costera que caracterizan al fenómeno El Niño.

5. Determinar las principales pautas espacio-temporales de variabilidad zooplánctica como respuesta al fenómeno El Niño.

5.1 Determinar la existencia de un acoplamiento biológico-ambiental como mecanismo de control de la productividad secundaria y la comunidad ictioplánctica durante el evento El Niño.

5.2 Determinar la prevalencia de los patrones de estacionalidad relacionados con la producción primaria y secundaria en la zona costera durante el evento El Niño.

5.3 Determinar el efecto de las alteraciones en los procesos costeros causados por el fenómeno El Niño en las pautas de distribución espacial del zooplancton y la comunidad ictiplánctica.

6 Caracterizar la dinámica interanual y estacional de las asociaciones de larvas de peces como efecto del fenómeno El Niño.

6.1 Determinar el efecto del evento El Niño en la diversidad de larvas de peces.

6.2 Determinar las pautas más parsimoniosas de ordenación de las asociaciones de larvas de peces y su variación estacional e interanual.

6.3. Modelar la respuesta de los taxa más dominantes de larvas de peces ante los cambios ambientales más característicos del evento de El Niño.

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Capítulo 2

Consideraciones Metodológicas

Consideraciones metodológicas

2.1 Área de estudio

El área de estudio comprende la franja de la plataforma continental que se extiende aproximadamente desde Punta Farallón en el estado de Jalisco (19°19'77"N y 105°00'28"W) hasta Cuyutlán, Colima (18°58'24"N y 104°13'51"W), (figura 1). La línea de la costa es irregular y comprende las bahías de Tenacatita y Navidad y el complejo de Santiago-Manzanillo, el resto de la línea de costa está formado por playas relativamente extensas y poco protegidas (Godínez-Domínguez y González-Sansón, 1998). La plataforma continental de esta región es muy estrecha, si se limita a la isóbata de 200 m su anchura es tan sólo de 7-10 km (Filonov et al. 2000).

La dinámica hidrológica de la costa de Jalisco y Colima está determinada por un flujo con dirección noroeste en verano y suroeste en invierno (Pacheco-Sandoval 1991; Badan 1997). En invierno y primavera el área está dominada por la Corriente de California, la cual está mezclada con la Contracorriente Ecuatorial y la Corriente Norecuatorial entre los 15° y 20°N. En verano y otoño la Corriente de California se debilita y el área se ve influenciada por un flujo de agua tropical transportado por la Contracorriente Ecuatorial a través de la Corriente Norecuatorial y la Corriente Costera de Costa Rica (Wyrtki 1965; Pacheco-Sandoval 1991). Durante junio y julio la Corriente

Costera de Costa Rica fluye al norte siguiendo la costa de Centroamérica y México y llega hasta Cabo Corrientes (Wyrtki 1965).

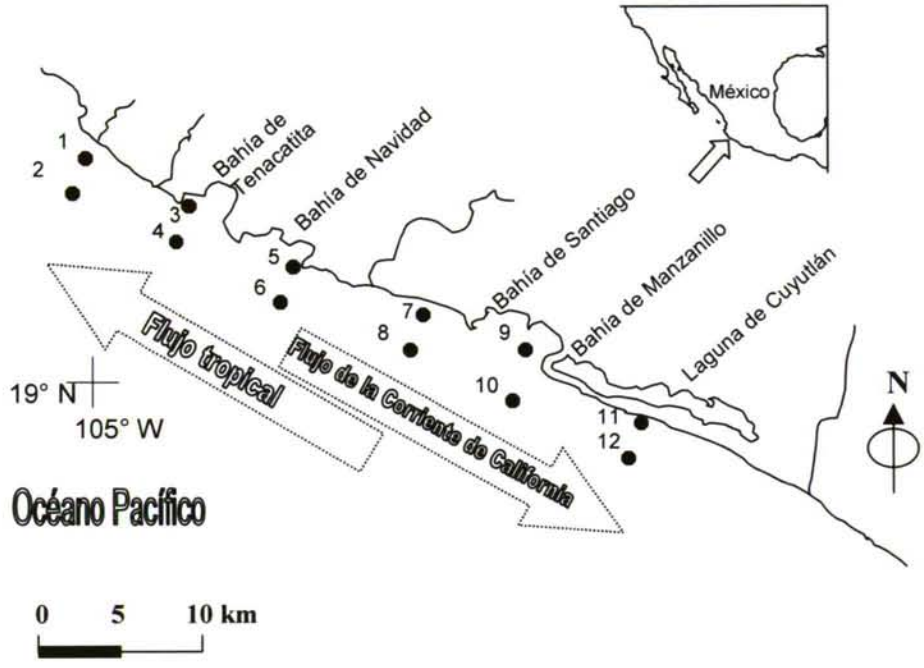

Figura 1. Área de estudio. Los puntos señalan la ubicación de las estaciones de muestreo.

Como en muchas otras regiones del Océano Pacífico, la circulación superficial local está influenciada estacionalmente por cambios en los

vientos. Desde finales del otoño y principios de primavera los vientos son fuertes y provienen del Norte por lo que las aguas fluyen hacia el Sur; en verano y principios de otoño los vientos dominantes provienen del Sur y llevan agua tropical superficial hasta el interior del Golfo de California (Thunell et al. 1994; 1996).

2.2 muestreos de zooplancton

Se realizaron arrastres zooplánctícos mensuales en las 12 estaciones de muestreo durante 27 meses (tablas 1 y 2), desde diciembre de 1995 hasta diciembre de 1998. El muestreo se efectuó a bordo del barco de investigación pesquera BIP-V. Los muestreos de zooplancton se realizaron siguiendo la metodología propuesta por Smith y Richardson (1977), y fueron realizados durante la noche con una duración de arrastre de 5.34 a 8.99 minutos por estación, dependiendo de la profundidad registrada. Los muestras se recolectaron con una red Bongo de 0.505 mm de apertura de malla, 3.0 m de manga y 0.6 m de diámetro de boca mediante arrastres oblicuos con trayectoria semicircular, a profundidades que variaron desde los 86 m hasta la superficie según la batimetría de cada estación de muestreo. A la red se le adaptó un flujómetro digital para medir el volumen de agua filtrado. El material recolectado fue fijado con formaldehído al 4% y una solución saturada de borato de sodio (Griffiths et al. 1976).

Tabla 1 Profundidad (m) de los sitios de muestreo y de los arrastres planctónicos realizados en la Costa de Jalisco y Colima.

Sitios	Latitud	Longitud	Profundidad Real	Profundidad de arrastre	% de la columna muestreado
1	19°16´645"N	104°55"765"W	60.0	44.7	74.5
2	19°15'898"N	104°56'216"W	126.0	77.2	61.2
3	19°14'173"N	104°51'206"W	60.9	44.7	73.3
4	19°13'086"N	104°52'922"W	94.8	64.1	67.6
5	19°10'744"N	104°44'022"W	60.0	48.0	80.0
6	19°09'398"N	104°32'657"W	93.0	85.0	91.3
7	19°07'215"N	104°31'855"W	60.4	44.0	72.8
8	19°06'163"N	104°32'343"W	120.9	79.4	65.6
9	19°01'653"N	104°20'839"W	61.0	43.6	71.4
10	19°00'547'N	104°21'213"W	96.5	60.7	62.9
11	18°59'647"N	104°17'809"W	60.3	42.0	69.6
12	18°58'577"N	104°18'817"W	132.7	86.8	65.4

2. 3 Muestreos de fitoplancton

Sólo durante 1998 y de manera simultanea a los arrastres de zooplancton, se tomaron muestras de agua con una botella Niskin a 0 y 25 m de profundidad. Con un microscopio invertido y cámaras de sedimentación de 15 ml se identificaron los organismos y se determinó la abundancia de diatomeas y dinoflagelados por el método de Utermöhl (Hasle 1978). Los conteos fueron estandarizados a número de células por litro de agua.

Tabla 2. Distribución temporal de los cruceros para la colecta de muestras de zooplancton en la costa de Jalisco y colima. El fondo sombreado indica los meses en que se realizaron cruceros. Las muestras de zooplancton solamente fueron colectadas durante 1998.

1995	1996	1997	1998
enero	enero	enero	enero
febrero	febrero	febrero	febrero
marzo	marzo	marzo	marzo
abril	abril	abril	abril
mayo	mayo	mayo	mayo
junio	junio	junio	junio
julio	julio	julio	julio
agosto	agosto	agosto	agosto
septiembre	septiembre	septiembre	septiembre
octubre	octubre	octubre	octubre
noviembre	noviembre	noviembre	noviembre
diciembre	diciembre	diciembre	diciembre

2.4 Estandarización de biomasa zooplánctica y abundancia de larvas de peces

La determinación de biomasa zooplánctica fue realizada siguiendo el método de volumen desplazado descrito por Beers (1976; 1981). Los zooplánctereres más grandes de 3 cm fueron excluidos de las muestras. Los valores de biomasa se estandarizaron a unidades de centímetros cúbicos (cm^3).

Los valores de la abundancia de cada espécimen por muestra fueron normalizados a un número de organismos en 10 m^2 de superficie marina (Smith y Richardson 1977), utilizando la siguiente fórmula:

$$C = 10\ (a^{-1}\ b^{-1}\ c\ d)$$

donde:

C = número de larvas en 10 m^2

a = superficie del aro de la red $\pi\ r^2 = 3.1416\ (0.3)^2 = 0.2827\ m^2$

b = f (r), f = factor de calibración del flujómetro, r = número de revoluciones del flujómetro durante el arrastre

c = número de larvas obtenidas en el contaje

d = longitud de cable filado (m) y tangente promedio del ángulo del cable durante el arrastre.

2.5 Taxonomía de larvas de peces

Las larvas de peces se identificaron hasta el menor nivel taxonómico posible, para lo que se valoraron los caracteres merísticos, morfométricos y de pigmentación. Se identificaron 92304 larvas de peces provenientes de 316 muestras de zooplancton.

Para la identificación general de las especies, se utilizaron principalmente los trabajos de Leis y Rennis (1983) y Moser (1984; 1996), así como la literatura especializada para cada taxón: Yoshida (1979) y Richards (1989) para la familia Scombridae, Moser et al.

(1977) para Scorpaenidae, Sumida et al. (1985) para Carangidae y Smith (1979) para larvas leptocéfalas. Con la finalidad de identificar las larvas de peces hasta nivel específico, el proceso se complementó con el dibujo, la tinción y aclaración de los especimenes (Potthoff 1984).

Una vez identificadas las larvas de peces, se establecieron las unidades taxonómicas operativas, que son consideradas como entidades independientes, cada una de estas entidades se les denominó Taxón. Es necesario mencionar que dentro del listado taxonómico se incluyen larvas de peces identificadas hasta nivel de género, especie y morfotipos. Se consideraron como morfotipos (a nivel género o familia) los organismos que no pudieron identificarse más allá del género o de la familia pero que se distinguen como una identidad distinta de acuerdo a sus características morfológicas, merísticas y pigmentarias. A cada morfotipo se le asignó una letra (eg. Gobidae Tipo A, B, *Symphurus* sp.a, b,). En los apéndices I, II y III se muestran las abundancias mensuales de cada taxa.

Algunas larvas de las familias Antennaridae, Bramidae, Congridae, Diodontidae, Gempilidae, Haemulidae, Kiposidae, Labridae, Melemphaidae, Moringuidae, Myctophinae, Paralepididae, Priacantidae, Sciaenidae y Triprerygiidae, no se incluyen en el listado taxonómico debido a que únicamente fue posible identificarlas al nivel de familia, sin embargo se realizaron descripciones detalladas de los especimenes y morfotipos para su posterior identificación. (Ver el

Anexo I "Fish larvae off Jalisco and Colima coastal waters: a catalogue; que acompaña la presente tesis).

2.6 Muestreos hidrográficos

Se realizaron dos tipos de muestreos hidrográficos. 1) El primero se realizó de manera simultanea con cada muestreo de zooplancton y es el que se detalla a continuación. Se realizaron sondeos verticales de la columna de agua con un dispositivo CTD-SBE 19 Sea Bird Prolifer previamente a los arrastres de zooplancton. La red de estaciones consistió en los 12 puntos que se muestran en la figura 1, situados en la plataforma continental y separados de la línea de la costa entre 3 km (estaciones cercanas) y 4.5 km (alejadas) a profundidades aproximadas de 60 y 132 m (tabla 1). Las tendencias temporales de temperatura y salinidad superficiales se analizan a través de los valores promedios mensuales a 10 m de profundidad. 2) Se realizaron una serie de levantamientos oceanográficos continuos (16-18 horas) a una velocidad de 6-7 nudos. Cada serie estuvo compuesta por 10 transectos perpendiculares a la costa con una distancia entre ellos de 1.5 km, en los que se realizaron 10 sondeos verticales hasta la profundidad máxima de 150 m. Estos levantamientos se realizaron en un área de 50 X 15 km (figura 2a) y se obtuvieron 100 perfiles verticales mensuales de temperatura y salinidad. Este estudio fue cambiado por un levantamiento en trayectoria cruzada de 80 X 15 km (figura 2b). El método de levantamiento Oceanográfico fue el descrito por Filonov et al. 1996 y

consiste en introducir el CTD en una estructura metálica con forma hidrodinámica que al ser remolcada da origen a una fuerza hidrodinámica de sustentación. El aparato (estructura y CTD) es arrastrado a velocidad máxima de 7 nudos con ayuda de un cable cuya longitud corresponde a la profundidad máxima necesitada, el aparato se encuentra apagado en la superficie del mar debido a la fuerza de sustentación, al llegar al punto de sondeo, sin disminuir la velocidad, la nave realiza uno o dos giros alrededor del aparato. Desde este momento el aparato pierde rápidamente la componente horizontal de velocidad y cae al fondo bajo la acción de su propio peso; simultáneamente se activa un interruptor de encendido con lo cual se inicia el registro de los parámetros. Con este método se realizaron un total de 29 levantamientos y se analizaron 2374 perfiles de temperatura y salinidad. La velocidad de caída del aparato se regula por su propio peso y por un peso muerto complementario, en este estudio fue cercan a 1 m/s, lo que permitió registrar perfiles con una discretización de 0.5 m.

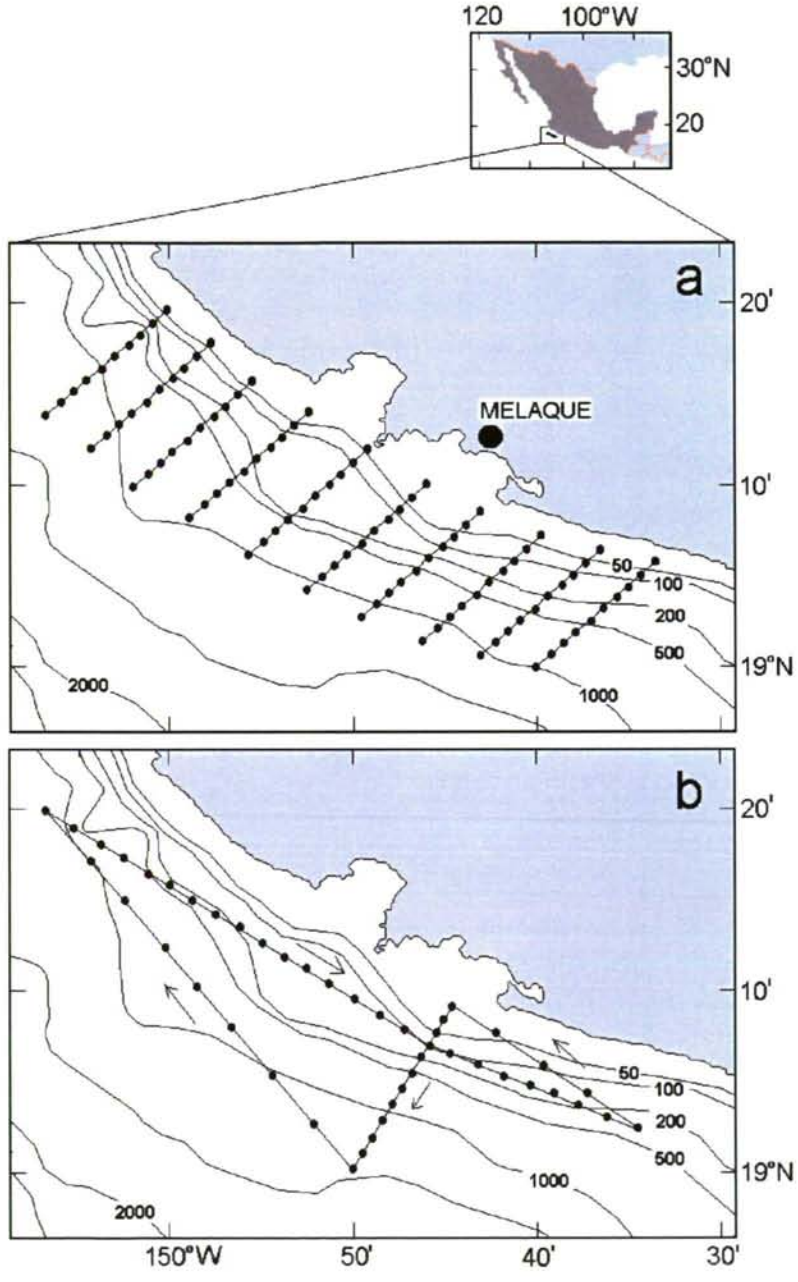

Figura 2. Posición de los transectos hidrográficos a) en el periodo 1996-1997 y b) en 1998. Los puntos señalan la posición de los sondeos verticales de temperatura y salinidad realizadas con un CTD ondulante.

2.7 Organización de la presentación de los resultados

En consecuencia con los objetivos de esta tesis, los capítulos 3, 4, 5 y 6 están orientados a determinar los patrones espaciales y estacionales típicos de la biomasa zooplánctica y la estructura y dinámica del ictioplancton durante un periodo normal, es decir, en ausencia de eventos ENSO (1995-1996). En los capítulos 6 y 7 se aborda la respuesta del plancton (fitoplancton, zooplancton, e ictioplancton) ante el efecto de El Niño 1997-98 y se determina la influencia de El Niño como fuente de variabilidad interanual.

Capítulo 3. se analizan las pautas de variabilidad de la biomasa zooplánctica, se determinan los patrones espaciales de su distribución y se determinan las pautas de estacionalidad. Se determina además la influencia de los procesos costeros a pequeña escala e hidroclimáticos en los patrones de productividad secundaria.

Capítulo 4. Analiza la abundancia de la comunidad ictioplánctica con especial énfasis sobre la abundancia de *Bregmaceros bathymaster*, especie más dominante. Se determinan las pautas espaciales y temporales de su distribución y se analiza la hipótesis de un acoplamiento entre los patrones hidroclimáticos, los ciclos de producción secundaria y los procesos costeros a meso y micro escala que determinan las pautas espaciales y los patrones de estacionalidad de la abundancia del ictioplancton.

Capítulo 5. Se analizan los patrones espaciales y estacionales de la diversidad a través de los indicadores más robustos e insesgados de la diversidad.

Capítulo 6. Se analiza las asociaciones de especies de larvas de peces y determina las pautas espaciales de segregación y los patrones estacionales de recomposición de dichas asociaciones. Además se determinan las especies que tipifican las diferentes asociaciones.

Capítulo 7. Se analiza de manera amplia los patrones de variabilidad oceanográfica y determina las pautas temporales de variabilidad más influyentes en el área de estudio; la variabilidad estacional y el evento de El Niño. Durante el periodo de El Niño se analiza el comportamiento estacional del fitoplancton para determinar una posible prevalencia del dinámica estacional normal durante el evento de El Niño. Se analiza el comportamiento interanual de la biomasa zooplánctica y la abundancia de larvas de peces, y se determinan patrones jerárquicos con las diferentes fuentes de variabilidad temporal (estacional e interanual), y se determinan los patrones de respuesta espacial de la distribución de las larvas de peces y la biomasa zooplánctica.

Capítulo 8. Se analiza los patrones interanuales de variabilidad de la diversidad y las asociaciones de larvas de peces. Se determinan la influencia del evento El Niño y la prevalencia de los patrones de

estacionalidad a través de indicadores estructurales de la comunidad ictioplánctica. Se analiza la relación jerárquica de las fuentes temporales de variabilidad y se determinan las variables oceanográficas que más explican esa variabilidad. Se tipifican las asociaciones de especies de larvas de peces de acuerdo a los patrones espaciales y temporales de variabilidad en sus diferentes escalas. Se analiza de manera integrada los procesos ecológicos relacionados con la respuesta de la productividad primaria secundaria y el ictioplancton ante la dinámica ambiental.

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Capítulo 3

Zooplancton biomass variability in the Mexican Eastern Tropical Pacific

Franco-Gordo, C. Godínez-Domínguez, E. & Suárez-Morales, E. (2001)
Pacific Science, 55(2), 191-202

Zooplankton Biomass Variability in the Mexican Eastern Tropical Pacific

Abstract

The time and space distribution of zooplankton biomass recorded during a year cycle (December 1995-1996) off the Pacific coast of central México is analyzed. Samples were obtained by surface (42-86m) oblique hauls at 12 sampling sites using a Bongo net. The overall average displacement volume biomass of zooplankton during the surveyed period was 1138 cm^3/1 000 m^3. Principal component analysis indicated that highest biomass concentrations occurred at coastal stations. The months with highest biomass values were those in which the lowest sea surface temperature values occurred (January-May). This was the same period in which the California Current was strongest and clearly influenced the hydrological conditions of the surveyed area. In these months, advective processes are active along the outer shelf, favoring upwelling of colder, relatively nutrient-richer waters that promote an overall local increase of zooplankton activity and populations. The high variability of biomass values is indicatative of episodic, localized processes that enhance productivity in the area.

key words: Secondary production, Eastern Tropical Pacific, Mexico.

3.1 Introduction

The zooplankton community represents a relevant link that transfers energy from primary producers to higher trophic levels in pelagic trophic webs (Baduini 1997). The patterns of distribution and abundance of zooplankton are affected by physical phenomena on very different spatial scales (Haury et al. 1978, Denman and Powell 1984). Physical factors include hydrographic events such as currents, wind stress, eddies, upwelling and stratification of the water column (Haury et al. 1978, Owen 1981).

One of the most frequently used parameters in evaluating the overall activity and density of this community is the measurement of biomass (Beers 1981). Seasonality and production cycles of zooplankton exhibit geographical variations and are determined by the availability of nutrients, hydrological conditions, and the dynamics of the zooplankton/ phytoplankton interactions (Heinrich 1962, Baduini 1997). Hence, the understanding of coupling of physical oceanic processes and zooplankton dynamics on a seasonal basis has been attempted in different areas of the Pacific Ocean but mainly in the California Current System (Chelton et al. 1982, Roesler and Chelton 1987, McGowan et al. 1996, Lavaniegos et al. 1998). The tropical area of the Mexican Pacific has received little attention and basic information on the zooplankton community is scarce.

Our study analyzes the space and time distributions of the neritic zooplankton biomass off the Pacific coast of central México in order to describe their dynamics and how they are influenced by the seasonal coastal current pattern, and advective process and other hydrological conditions.

3.2 Materials and methods

Zooplankton hauls were performed monthly during nighttime (2000 – 0700 hours) from December 1995 to December 1996. To avoid the considerable influence that small-scale hydrographic variability may have on the overall larval dispersal (Smith et al. 1999), all the trawls for a month were carried out during one night. Hauls were all oblique, at depths varying from 42 to 86 m. A standard Bongo net with 0.33- and 0.5- mm meshes and 0.6- m mouth diameter was used. A digital flowmeter was adapted to the mouth of the 0.5- mm net to estimate the amount of water filtered by this gear (Smith and Richardson 1979). Zooplankton samples were fixed and preserved in a 4% formalin solution, which was buffered later with sodium borate (Griffiths et al. 1976). Because of adverse climatic conditions, sampling was not possible during August and September 1996. Sea surface temperature (SST) and salinity were measured at each sampling site using a Seabird SBE19 CTD profiler.

Samples collected in the 0.5- mm net were immediately processed to obtain the zooplankton biomass to avoid volume changes associated with long-term preservation (Ahlstrom and Thrailkill 1963). Samples were processed according to the displacement volume method (Beers 1976). Organisms measuring over 3 cm in length were excluded from the samples; gelatinous zooplankters below this size were included in the biomass estimations. Estimated biomass values are reported as cm^3 per 1000 m^3 of filtered water.

Month-to-month variations in biomass were analyzed for all of the sampling sites. The monthly biomass values were averaged and a confidence range established according to Zar (1996). Month-to-month differences along the coast-oceanic gradient were evaluated using a Friedman Variance Analysis (Zar 1996). This method of analysis was selected because the distribution of biomass values in the area was not considered to be statistically normal. To determine the relation between zooplankton biomass values, temperature, and salinity, standard correlation tests were used. A Principal Component Analysis (PCA) was performed using biomass values from each sampling site and month (log data transformed). This was done to determine time/space distributional patterns of zooplankton biomass in the surveyed area.

3.3 Results

Monthly differences of zooplankton biomass during the survey period were statistically significant (X^2 = 76.24, n = 12, df = 10, $P < 0.005$). The highest biomass values were recorded during January, March, April and May. Biomass decreased in June and July and began to increase again in December (Figure 2*a*). The wide variation of confidence ranges indicates a high heterogeneity of biomass values throughout this period. Zooplankton biomass showed a significant tendency to decrease offshoreward (X^2 = 13.63, n = 66, df = 1, $P <$ 0.005). Maximum concentrations were recorded at stations near the coast (Figure 2*b*), which were also the shallowest (Table 1).

Table 1. Depth characteristics of Sampling sites

Sites	Latitude	Longitude	Depth bottom (m)	Depth trawl (m)	% sampled water column
1	19°16´645"N	104°55"765"W	60,0	44,7	74,5
2	19°15'898"N	104°56'216"W	126,0	77,2	61,2
3	19°14'173"N	104°51'206"W	60,9	44,7	73,3
4	19°13'086"N	104°52'922"W	94,8	64,1	67,6
5	19°10'744"N	104°44'022"W	60,0	48,0	80,0
6	19°09'398"N	104°32'657"W	93,0	85,0	91,3
7	19°07'215"N	104°31'855"W	60,4	44,0	72,8
8	19°06'163"N	104°32'343"W	120,9	79,4	65,6
9	19°01'653"N	104°20'839"W	61,0	43,6	71,4
10	19°00'547'N	104°21'213"W	96,5	60,7	62,9
11	18°59'647"N	104°17'809"W	60,3	42,0	69,6
12	18°58'577"N	104°18'817"W	132,7	86,8	65,4

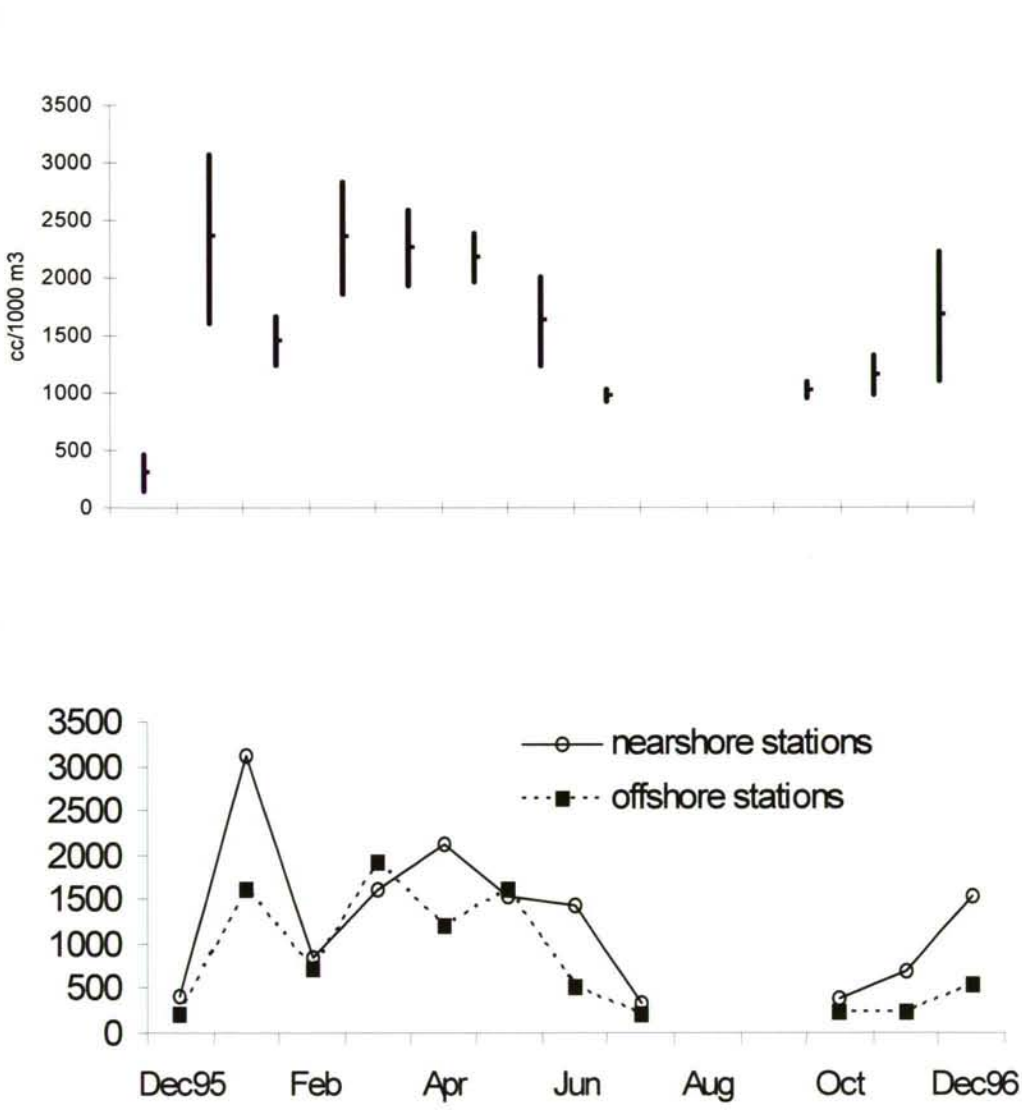

Figure 2. Monthly biomass distribution (*a*) mean and 95% CI and (*b*) in relation to coast proximity.

The ordination method used allowed verification of the differential behavior of zooplankton biomass values. The first component included the 68.5% of the variance in data and the second the 78.9% of the accumulated variance. Two distinct clusters were defined, the first one included winter and spring months (January-May), and the second one contained June-December (Figure 3*a*). February, June and December 1996 were located close to the origin between both clusters. June and December probably represent the transition time between two hydroclimatic periods (end and onset of the NECc and CC). These transitional periods could vary between years and one example of that is the difference in biomass values in two December months (1995 and 1996). February was the month with highest zooplankton biomass values and the highest variance. The PCA yielded two station groups: the first one (odd numbers), represented the near-shore sampling sites, whereas the second included off-coast stations (Figure 3*b*). The first component could be interpreted in both cases (months and stations) as hydrodynamic variability associated to coastal current pattern.

A significant and inverse relation (r = -0.61, P<0.005) was found between biomass and temperature at 10 m depth (Figure 4*a*). Salinity and zooplankton biomass were also significantly correlated (r = 0.38) (Figure 4*b*). Salinity and temperature of water at 10 m varied throughout the surveyed period (Figure 5).

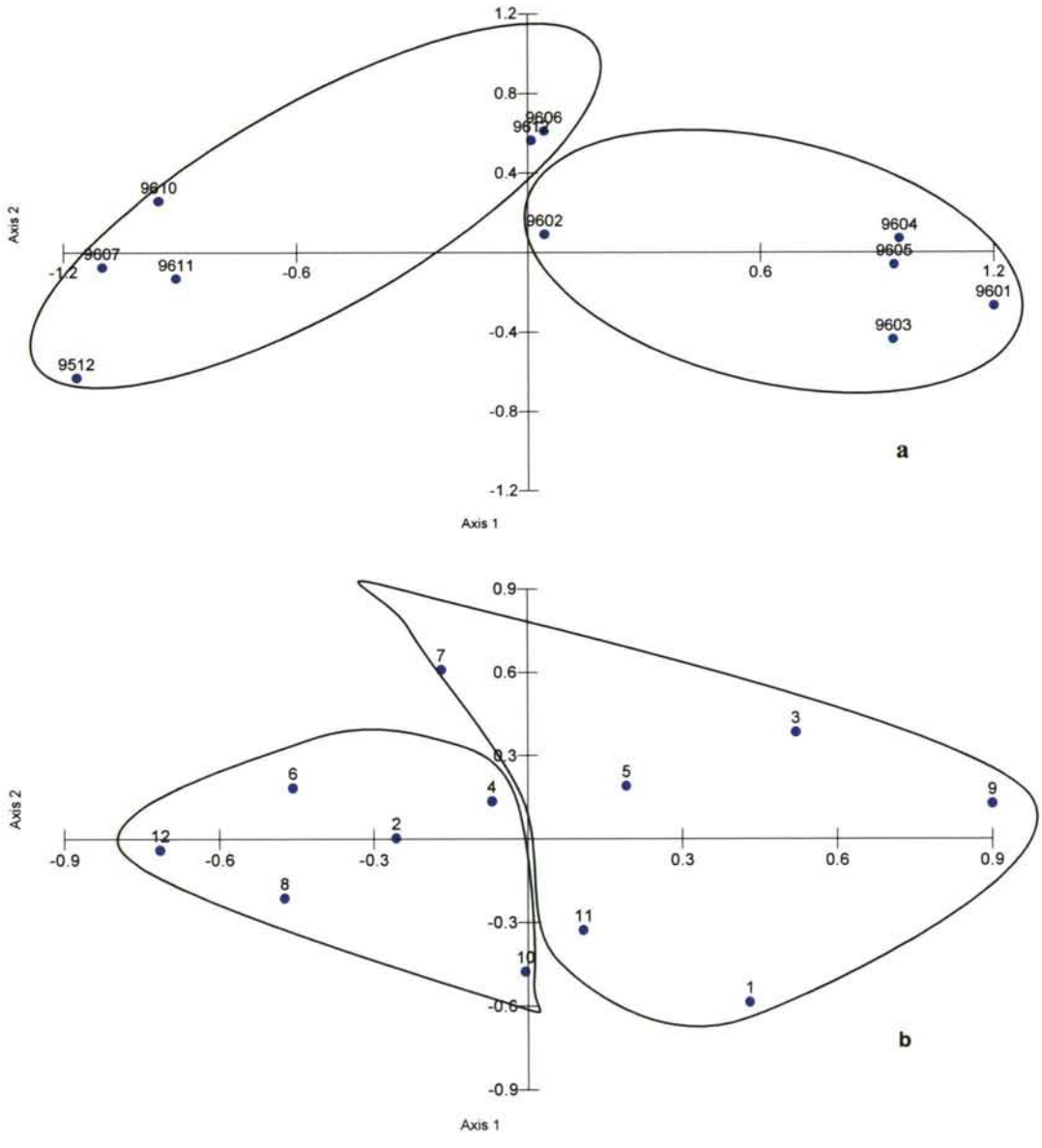

Figure 3. Principal component analysis of (*a*) sampling months (codes refer to year and month) and (*b*) station sampling (even numbers denote offshore stations; odd numbers denote nearshore stations).

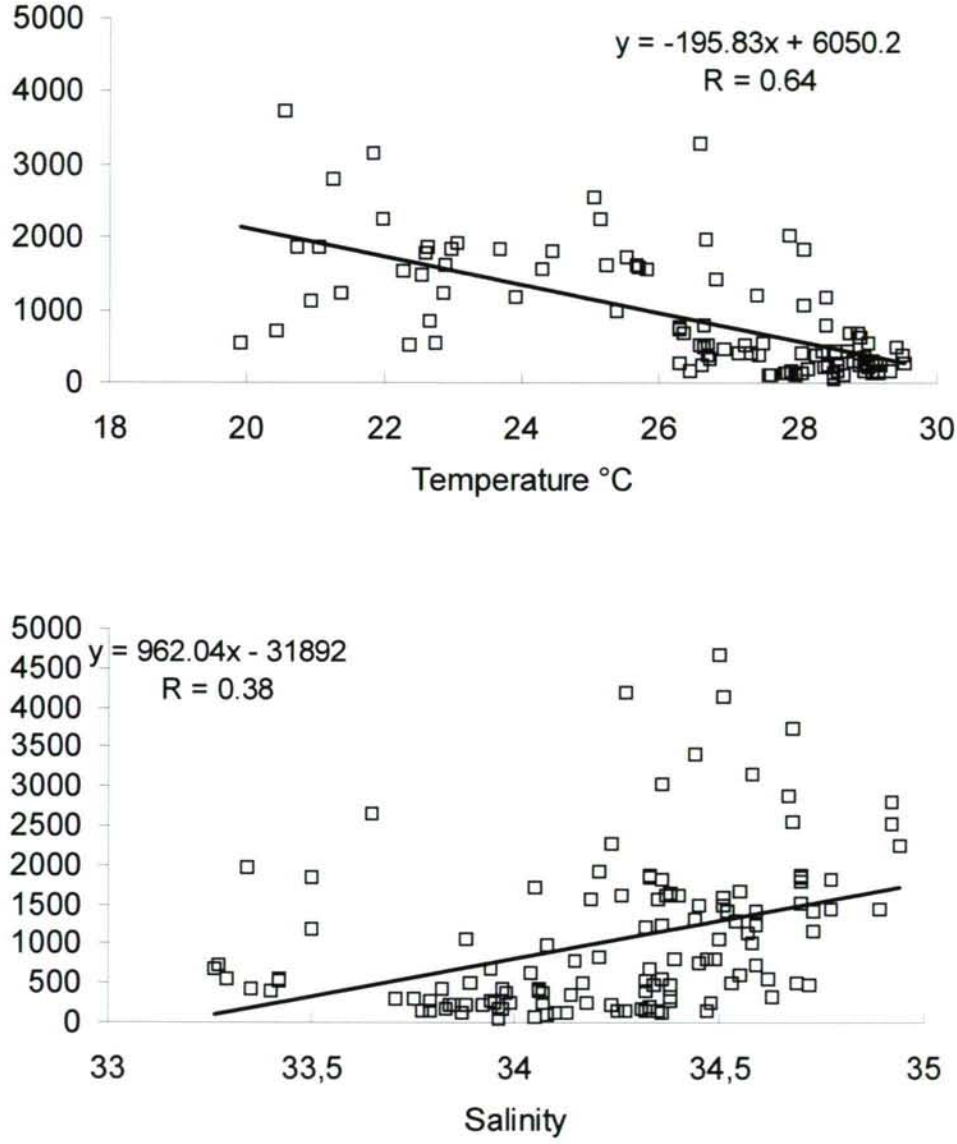

Figure 4. Relationship between biomass (cm^3/ 1000 m^3) and sea water temperature (*a*) and salinity (*b*).

Salinity exhibited relatively stable behavior between December 1995 and June 1996, with monthly average values ranging from 34.2 to 34.7 psu. Salinity decreased during the rainy season, with a minimum (33.4 psu) in October. Water temperature was lowest from January to May; March was the coldest month (21.4°C). Another thermic period was characterized by higher mean temperatures (26.3 to 29.2 °C), and included summer and autumn.

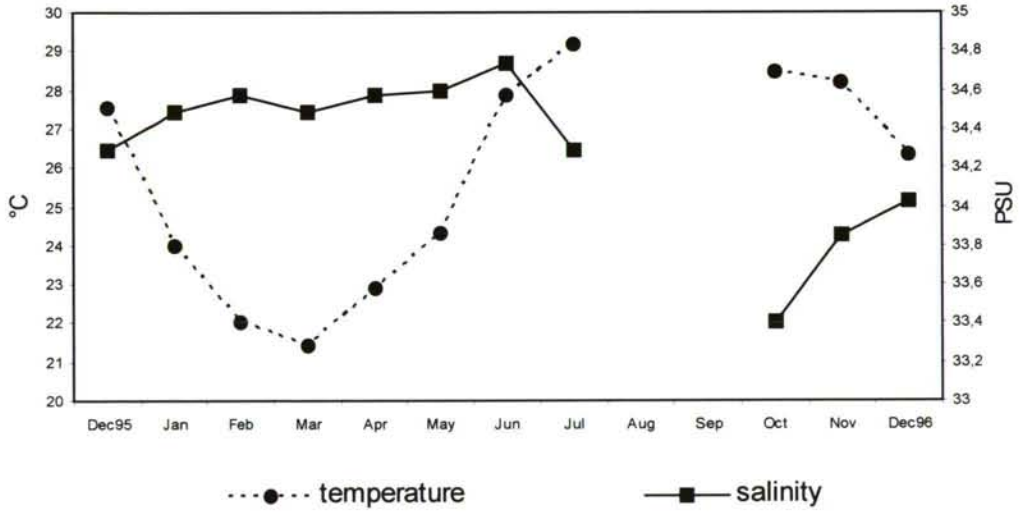

Figure 5. Temperature and salinity monthly averages recorded at 10 m depth.

Temperature profiles (Figure 6) during July are representative of tropical oceanographic conditions, with warm surface waters (29.7 °C SST) and a strong stratification with a deep thermocline. Contrasting

temperature profiles from March 1996 featured a thicker mixing layer, and lower SST (22.2 ºC) which are conditions related to the influence of the CC. During this season, coastal upwelling is produced by wind stress from the northwest that displaces water offshore and replaces it with nutrient-rich, cold water, from greater depths. The December profile is indicative of the end of the tropical season in the area, during which the influence of the NECc weakens and the progressive invasion of the CC is more evident (see Wyrtki 1965). The end of the influence of the CC in the area is indicated by the thermic profile from May, with the thermocline going deeper and with increasing SST values.

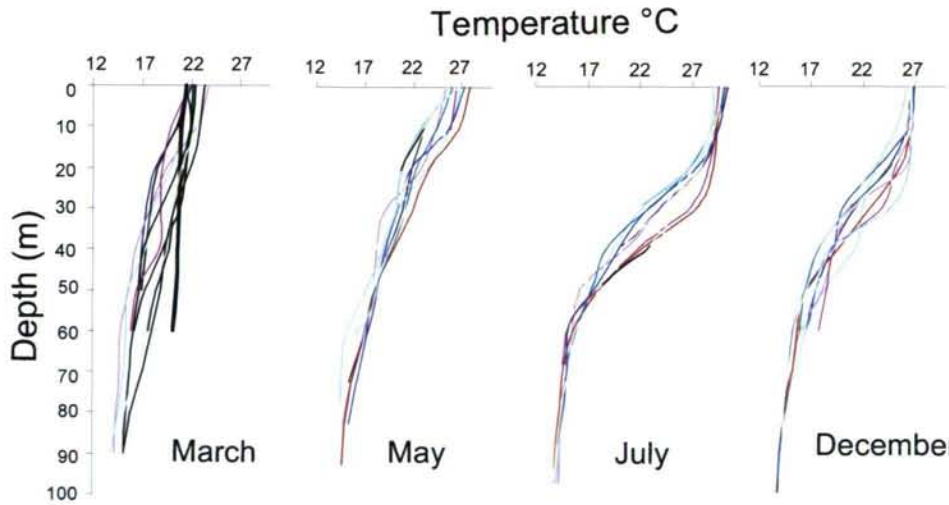

Figure 6. Temperature profiles of the main oceanographic seasons.

3.4 Discussion

Our data represents the first information on the month-to-month variation of zooplankton biomass during a year cycle in the coastal area of the Mexican Tropical Pacific. Biomass values showed a sharp two-season pattern during the survey period. Maximum average biomass values were recorded in the first season, between January and June. The second season was featured by relatively low mean biomass figures, and included the July-December period. A seasonal pattern of zooplankton productivity along the CC System has been recognized by several authors (Chelton et al. 1982, Roesler and Chelton 1987). Based on the analysis of a long-term series of zooplankton surveys in the central-western part of the Baja California peninsula, Lavaniegos et al. (1998) found highest biomass concentrations during summer (June through October). In general, the northern portion of the Gulf of California, has a nearly continuous high productivity level, the western coastal edge of the peninsula shows higher values during spring, and the eastern coast has increased biomass values in the autumn (Tunell et al. 1996). It is expected that these subtropical-temperate patterns will vary approaching lower, tropical latitudes, where biomass variations tend to be less pronounced (Suárez-Morales and Gasca 1994). In the oceanic region known as the Norequatorial Countercurrent Province of the Pacific, located off the coast of the Mexican section of the Eastern Tropical Pacific (see Longhurst 1998), two peaks of secondary production have been recognized. The first peak occurs in

winter (December-April or May), and the second in summer. This pattern has been observed for the southern part of the Baja California Hernández-Trujillo (1998) found the highest average values during winter and spring (over 250 cm^3/1 000 m^3), and lowest in summer and autumn (below 200 cm^3/1 000 m^3). This area is considered to be a transitional zone, but is still strongly influenced by tropical conditions. The pattern described by Hernández-Trujillo (1998) is consistent with the tendency shown by our biomass data throughout the year cycle.

The average zooplankton biomass recorded in the surveyed area was about four times higher than that reported by Hernández-Trujillo (1998) in the southern part of Baja California (240 cm^3/1 000 m^3). His highest values at 21°N are about 357 cm^3/1 000 m^3. McGowan et al. (1996) studied the long-term mean zooplankton biomass along the CC, and they reported most values as ranging between 200 and 800 cm^3/1 000 m^3. Our values are comparable to those reported by Brinton et al. (1986) (about 1 024 cm^3/1 000m^3) in the productive coastal areas of the Gulf of California, and by Jiménez-Pérez and Lara-Lara (1988) in the central Gulf of California (988 cm^3/1 000 m^3). Hence, the coastal areas of Colima and Jalisco have moderate to very high zooplankton biomass values, probably become of short-term, local events, as explained below.

The inverse behavior shown by the zooplankton biomass concentrations and the temperature values agree with several earlier reports (Colebrook 1977, Bernal 1979, 1981, Chelton et al. 1982,

McGowan 1984, 1985, Jiménez-Pérez and Lara-Lara 1988, McGowan et al. 1996, Lavaniegos et al. 1998) for the CC region. In all of these studies, highest zooplankton biomass episodes were correlated with low SST. According to our results and those of Filonov et al. (2000), the tropical coast of Mexico is influenced during winter by advective processes related to the CC. These processes promote coastal upwelling systems that enrich the surface layers, a well-known feature of the CC System (McGowan et al. 1996).

Previous surveys of the zooplankton variability of the CC System show strong links between zooplankton biomass and advective mesoscale processes (Bernal 1979, 1981, Bernal and McGowan 1981, Chelton et al. 1982, Lavaniegos et al. 1998). Those studies suggest that zooplankton biomass is sensitive to local changes in primary productivity that are due to advective processes, which affect nutrient impact (Roesler and Chelton, 1987). Periods of high secondary productivity in the Northeastern Pacific Ocean, and particularly in the CC System occur asynchronically or are episodic, spatially limited events (McGowan et al. 1996). According to Brodeur et al. (1996) the processes that enhance productivity tend to be localized and transient. Hernández-Trujillo (1998) stated that month-to-month variation of biomass values is very high in the area of Baja California; this seems to be true also for our study area. The erratic space distribution of highly variable biomass values found in our study, suggest that the major fluctuations of zooplankton biomass during the surveyed period are more related to hydrological-physical

processes than to strictly biological factors, at least in the holoplankton. Hence, the high month-to-month variability of our data, and particularly the very high isolated values (over 1 500 cm^3/1 000 m^3), seem to confirm the idea of temporal and spatial patchiness, even in more tropical areas such as our the survey area.

The abundance of ichthyoplankton in the same survey area (Franco-Gordo et al. 2000) exhibited a behavior similar to the zooplankton biomass in terms of distribution in time and space. Variations in zooplankton abundance can affect larval fish populations in several ways, and a positive correlation is expected when zooplankton is visualized as food for fish larvae (McGowan et al. 1996). However, interactions between trophic levels seem to be more complex, and data suggest that a lag of several months occurs between peaks in abundance of zooplankton and fish larvae. In tropical zones, such as the survey area, with a more diverse assemblage of species and different dynamics, it seems reasonable to expect that this lag may be reduced. Lucano-Ramírez (1999) and Santamaría-Miranda et al. (1995) stated that the reproductive season of some of the commercially relevant species in the area occurs from November to April (winter), perhaps coinciding with increased food availability for their larvae. Mullin and Cass-Clay (1997) noted an overall correlation between the abundance of the larvae of the Pacific hake and zooplankton biomass. Thus, the reproductive strategies of some of the fish species dwelling in the Mexican Tropical Pacific appear to be linked to peaks in primary and secondary productivity in these areas.

Some authors have suggested that coastal upwelling processes, besides favoring a local enrichment of the water, could have a relevant role in transporting zooplankters coastward. This effect would increase the chances of larvae reaching shallow coastal, potentially richer, or even nursery zones (Pitts 1999). However, during summer, with a deep thermocline, the riverine or coastal freshwater input in the zone could also produce an enrichment of the coastal systems and promote an increase in zooplankton biomass. Ekman transport during upwelling periods, together with the daytime migration patterns shown by some zooplankton groups (Zaret and Suffern, 1976), could result in a differential distribution related to both depth and distance offshore (Pitts 1999).

To reduce sampling bias related to zooplankton migration cycles and emphasize physical, hydrological effects, all of our samples were taken at night and include up to 71% of the water column. Therefore, the variability of biomass observed in this survey could be attributed to the effect of physical, hydrological conditions rather than to migrational patterns.

Pronounced interannual variability of the distribution of zooplankton biomass has been demonstrated in the CC System (McGowan et al. 1996) and even in transitional areas such as the southern part of the Baja California peninsula (Hernández-Trujillo, 1998). Although a general pattern has been established in our survey area, further

studies are needed to refine interpretations of fluctuations in zooplankton biomass in this tropical zone.

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Capítulo 4

A seasonal survey of the fish larvae community of the central Pacific coast of México

Franco-Gordo, C., Suárez-Morales, E., Godínez-Domínguez, E. & Flores-Vargas, R. (2001). *Bulletin of Marine Science*, 68, 383-396.

A SEASONAL SURVEY OF THE FISH LARVAE COMMUNITY OF THE CENTRAL PACIFIC COAST OF MEXICO

Abstract

Larval fish abundance off the coasts of the central portion of the Mexican Pacific was studied during a year cycle. Zooplankton samples were collected during 11 sampling cruises carried out between December 1995 and December 1996 using a bongo net. A total of 63,342 larvae were collected. The most abundant families were Bregmacerotidae 94.6%, Eleotridae 1.19%, Sciaenidae 0.67%, and Engraulidae 0.64%. Abundance values were significantly higher ($P < 0.005$) at near-shore stations, suggesting a potential ecological use of adjacent coastal environments as nursery areas. Fish larvae were most abundant during January-May, a period with the lowest average sea temperature, which is related to the seasonal influence of the California Current (CC). In these months, advective processes are active along the outer shelf favoring upwelling of colder, relatively nutrient-richer waters which in turn allow an overall local increase of zooplankton activity and populations. The high variability of abundance values in the surveyed area suggest episodic, localized processes enhancing the local productivity. Lowest abundance occurred in October-December, when the CC is weak and the area is influenced by tropical oligotrophic waters. Highest abundance values were consistently found at nearshore stations, this is probably related

to 1) the extraordinary dominance of the coastal species *Bregmaceros bathymaster* and 2) the inshoreward transport of larvae into potential nursery areas. *B. bathymaster* was the most abundant larvae during the entire survey period. It is suggested that this species has a year-round breeding cycle, with moderate month-to-month but sharp seasonal variations. The absences of adult individuals of this species in the surveyed area suggest that it probably spawns in the ocean and its larval stages are transported inshorewards into potential nursery zones.
Key words: advection, larval transport, ichthyoplankton, bregmacerotidae, Pacific, Mexico

4.1 Introduction

Studies on basic aspects of the pelagic environment such as the composition, distribution, and abundance of ichthyoplankton during different seasons can yield relevant information about the factors affecting the community during a year cycle. This is particularly relevant in tropical areas which tend to have undefined seasonal cycles. The knowledge of the ichthyoplankton dynamics and ecology is a basic tool to infer patterns of the life history and distribution of adult fish and to determine areas and seasons of spawning and recruitment (Leis and Rennis, 1983; Richards and Vásquez-Yeomans, 1996; Vásquez-Yeomans and Richards, 1999).

Bregmacerotids has been described as one of the 10 most abundant fish families in both, neritic and oceanic waters of the tropical and subtropical regions (Houde, 1984). The group includes only one multispecific genus, *Bregmaceros*. Although widely distributed, larvae of Bregmacerotidae are not abundant north of 21°N in the Pacific Ocean, their average density in the California area has been estimated to be around 1-4 org 10 m^{-2}, with highest densities during June (Moser et al., 1993). *Bregmaceros bathymaster* (Jordan and Bollman, 1890) is a tropical-subtropical form and one of the commonest species of the genus in the Eastern Tropical Pacific (Stevens and Moser, 1996). It is distributed between the 40°N-40°S, adults and larvae have been found to be abundant in the Gulf of Panama (D'Ancona and Cavinato, 1965) and in adjacent regions of the Pacific, including the Gulf of California (Moser et al., 1973). In the Eastern Tropical Pacific, larvae of this species have been recorded by Ahlstrom (1971, 1972), Belyanina (1974), and Acal (1991). However, there are no previous studies dealing with the seasonal behavior of this species in the Mexican Pacific, an area recognized by the lack of ichthyoplankton studies (Ahlstrom, 1972; Acal, 1991). The seasonal variability of the abundance of the ichthyoplankton collected along the central portion of the Mexican Pacific during a year cycle is described herein. Abundance is analyzed as related to the general hydrographic conditions of the area thoughout the year cycle. Special reference is made on the abundance of *B. bathymaster* larvae.

4.2 Material and Methods

The sampling grid consisted of 12 sampling stations (Fig. 1 chapter 2). The zooplankton samples were collected monthly from December 1995 through December 1996, on board the BIP-V oceanographic vessel. No sampling was made in August and September 1996 because of adverse climatological conditions. Samples were obtained using a Bongo net with mesh sizes of 0.5 and 0.33 mm. Plankton hauls were oblique, from 42-86 m to the surface at each station, all of them over the continental shelf. Zooplankton hauls were performed monthly during nigthtime (20:00-07:00 hrs.) only. Hauls were made for as long as 5.34 – 8.99 minutes per station. A digital flowmeter was adapted to the net mouth in order to estimate the amount of water filtered by the net (Smith & Richardson, 1979). Samples were fixed and preserved in a 4% formaline solution buffered with sodium borate (Griffiths et al., 1976).

Temperature and salinity were measured at each station with a Seabird CB19 CTD profiler. Fish larvae were sorted out from the 132 original zooplankton samples collected during the 11 sampling cruises. This was performed on the 0.5 mm net plankton only; abundance was standardized into number of larvae under 10 square meters (Smith and Richardson, 1979). With these values a data matrix was built in order to perform the statistical analysis of numerical data. Monthly abundance data were then averaged and their Confidence Range was determined (Zar, 1996). Assuming non-

normality of the abundance values, a non-parametric ANOVA by range of Friedman (Zar, 1996) was used to analyze the month-to-month variations of larval abundance, as related to near-coast *vs* off-coast stations. A one-way non-parametric ANOVA was used to evaluate larval abundance in relation with salinity and temperature values. Principal component analyses were used to determine seasonal and spatial patterns of larval abundance.

4.3 Results

Salinity and temperature of water at 10 m showed variations throughout the surveyed period (Table 1). Salinity showed a relatively stable behavior between December 1995 and June 1996 with monthly average values ranging from 34.2 to 34.7 psu. Salinity decreased during the rainy season, with a minimum (33.4 psu) in October. Relatively low temperature values characterized a cold season from January to May, March being the coldest month (21.4°C). Another thermic period was featured by higher temperature averages (26.3 to 29.2 °C), and it included summer and autumn. Temperature profiles (Fig. 1) during July are representative of tropical oceanographic conditions, with warm surface waters (29.7 ºC SST) and a strong stratification with a deep thermocline. March profiles featured contrasting conditions, with a thicker mixing layer, and lower SST (22.2 ºC). These conditions are related to the influence of the California Current. During this cold season, coastal upwelling is produced by stress winds from the NW which displaces water

offshore and replaces it with nutrient-rich deeper cold water. The December profile is indicative of the end of the tropical season in the area, during which the influence of the Norecuatorial Current weakens and the progressive onset of the California Current conditions is more evident (see Wyrtky, 1965). The end of the influence of the California Current in the area is indicated by the thermic profile of May, with increasing SST values and a deeper thermocline.

Table 1. Monthly results of abundance larvae, temperature and salinity

Mounth	Mean *	Std. Dev.	Temperature **	Salinity **
December'95	1505,58	1691,89	27,54	34,26
January	2402,66	1709,19	25,20	34,40
February	7941,00	6591,51	23,80	34,40
March	2695,33	1845,75	21,39	34,48
April	2532,16	2622,27	22,80	34,57
May	4953,08	4194,97	24,33	34,59
June	1694,50	1040,98	27,88	34,74
July	1143,00	734,49	29,17	34,28
October	422,66	271,99	28,49	33,40
November	494,33	397,57	28,17	33,85
December'96	412,08	287,41	26,34	34,99

* Number of larvae/10m2

** 10 m depth

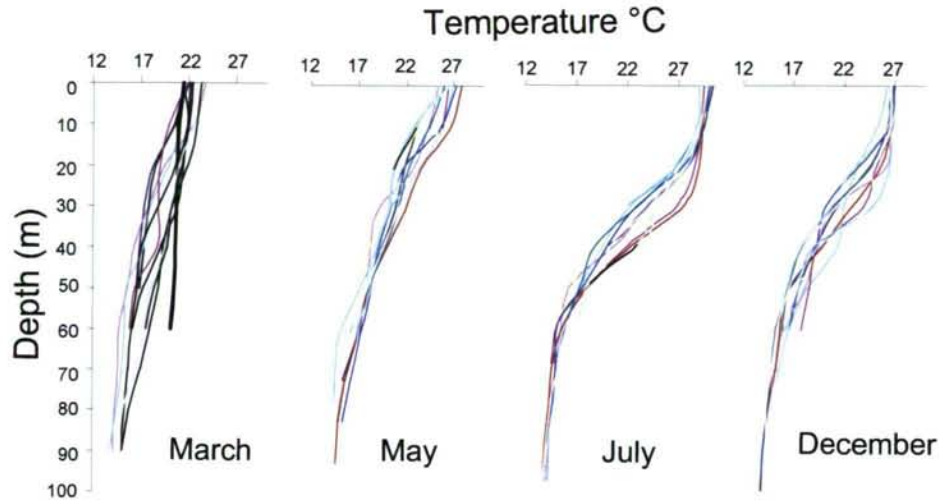


Figure 1 Temperature profiles characteristic of the oceanographic seasonality of coastal Mexican Tropical waters.

A total of 63,342 (314,357 larvae/10m^2) fish larvae were sorted from all zooplankton samples collected. The taxonomic identification of the fish larvae collected in the area yielded a total of 54 families. Up to 62,379 larvae were identified to the species or genus level, which represents 98.42% of the total fish larvae caught, 742 larvae were identified to the family level (1.17%), and only 221 larvae (0.34%) remained unidentified (Table 2). Highest differences in abundance were found between families (Table 3). The family Bregmacerotidae was represented by *Bregmaceros bathymaster* only, with an overall annual abundance of 295,036 larvae 10m^{-2}. Only the Eleotridae showed a relative abundance over 1%. Hence, overall variability of fish larvae abundance during the survey period was given mainly by

the abundance of *B. bathymaster*, which represented between 77 and 98% of the total fish larvae abundance during the months surveyed. Its abundance varied from 3,789 larvae $10m^{-2}$ in October, to 93,538 larvae $10m^{-2}$ in February (Fig. 2). Highest overall abundance was recorded during February (95,042 ± CI 3,729 larvae $10m^{-2}$), May (59,337 ± CI 2,373 larvae $10m^{-2}$), March (32,279 ± CI 1,044 larvae $10m^{-2}$), and April (30,328 ± CI 1,483 larvae $10m^{-2}$). Up to 70% of the total annual catch was collected during these four months. Lowest overall abundance was recorded in the October-December period (4,900-5,650 larvae $10m^{-2}$), which represented only 4.9% of the total annual fish larvae numbers (Table 2).

Table 2. Total fish larvae abundance monthly sampled on Jalisco and Colima coast.

Month	Key	larvae/10m²	Larvae Occurrence	Specific Level	Family Level	Unidentified	Damaged
December'95	JALCO-9512	17907	3493	3416	43	26	8
January	JALCO-9601	28811	5227	5196	27	2	2
February	JALCO-9602	95042	18739	18636	55	48	0
March	JALCO-9603	32279	7384	7361	9	13	1
April	JALCO-9604	30328	5637	5410	216	11	0
May	JALCO-9605	59337	13131	13057	51	14	9
June	JALCO-9606	20160	3465	3326	122	17	0
July	JALCO-9607	13561	2625	2517	78	30	0
October	JALCO-9610	4969	1228	1157	47	24	0
November	JALCO-9611	5643	1437	1342	80	12	3
December'96	JALCO-9612	4960	976	961	14	1	0
	TOTAL	**314357**	**63342**	**62379**	**742**	**198**	**23**

The overall larval abundance showed two different patterns during the annual cycle (X^2 = 72.4, P < 0.005) . The first one, between January and May, was featured by the highest abundance of larvae. It included up to 78% of the total catch, and was related to the months with lowest SST values. The second period (June-December) showed lower abundance values, represented 22% of the total fish larvae numbers, and is related with the warmest months (Fig. 3*a*). Spatial patterns were discriminated and the distance from coast was the main gradient identified (Fig. 3*b*).

Highest larval abundance values were consistently recorded in the coldest months and were related also to the stations nearest to the coast (stations 1, 3, 5, 7, 9 and 11). The annual average abundance estimated for these near-shore localities was over 3,028 (± CI 983) larvae $10m^{-2}$ whereas the figure was slightly over 1,734 (± CI 564) larvae $10m^{-2}$ in the remaining stations (Fig. 4). Differences were significant (X^2 = 16.6, P < 0.005) during the months, although highest differences were found during the coldest period (January to May).

Significant differences between larval abundance and environmental variables were found (Fig. 5). Temperature (X^2 = 16.3, P < 0.05) and salinity (X^2 = 11.1, P < 0.05), and a normal model explains in a better way the abundance distribution, temperature (K.S. dn = 0.14, P>0.5) and salinity (K.S. dn = 0.25, P>0.5).

Table 3. Relative importance of fish larvae families in organisms number.

Family	Frequency	Larvae/10m^2	F (%)	F Accumulate
Bregmacerotidae	59448	295036	94.62	94.62
Eleotridae	784	3757	1.19	95.81
Sciaenidae	419	2178	0.67	96.48
Engraulidae	403	2029	0.64	97.12
Clupeidae	367	2069	0.58	97.70
Gobiidae	228	1599	0.36	98.07
Scombridae	188	937	0.30	98.37
Phosichthyidae	169	909	0.27	98.64
Cynoglossidae	122	606	0.19	98.83
Myctophidae	98	494	0.16	99.00
Paralichthyidae	95	369	0.15	98.98
Carangidae	79	375	0.13	99.26
Labridae	66	322	0.11	99.36
Lutjanidae	34	139	0.05	99.42
Pomacentridae	31	352	0.05	99.47
Scorpaenidae	28	186	0.04	99.51
Tetraodontidae	26	178	0.04	99.55
Labrisomidae	24	167	0.04	99.59
Balistidae	22	109	0.04	99.62
Sphyraenidae	22	118	0.04	99.66
Gerridae	21	143	0.03	99.69
Nomeidae	19	115	0.03	99.72
Gobiesocidae	18	73	0.03	99.75
Synodontidae	17	87	0.03	99.78
Porichthydae	16	69	0.03	99.80
Haemulidae	15	91	0.02	99.83
Congridae	13	69	0.02	99.85
Ophidiidae	11	52	0.02	99.87
Moringuidae	10	51	0.02	99.88
Ophichthidae	9	45	0.01	99.90
Apogonidae	9	36	0.01	99.91
Hemiramphidae	6	30	0.01	99.92
Serranidae	6	12	0.01	99.93
Bothidae	6	32	0.01	99.94
Mugilidae	6	25	0.01	99.95
Elopidae	5	21	0.01	99.96
Blenniidae	3	13	0.00	99.97
Ammodytidae	3	14	0.00	99.97
Albulidae	2	6	0.00	99.98
Atherinidae	1	4	0.00	99.98
Opistognathidae	1	6	0.00	99.98
Paralepididae	1	5	0.00	99.98
Carapidae	1	3	0.00	99.98
Fistularidae	1	6	0.00	99.98
Antennaridae	1	4	0.00	99.99
Kyposidae	1	5	0.00	99.99
Priacantidae	1	5	0.00	99.99
Dactyloscopidae	1	3	0.00	99.99
Bramidae	1	3	0.00	99.99
Melanostomidae	1	5	0.00	99.99
Bathylagidae	1	3	0.00	100.00
Exocoetidae	1	6	0.00	100.00
Melanocetidae	1	5	0.00	100.00
Muraenidae	1	4	0.00	100.00

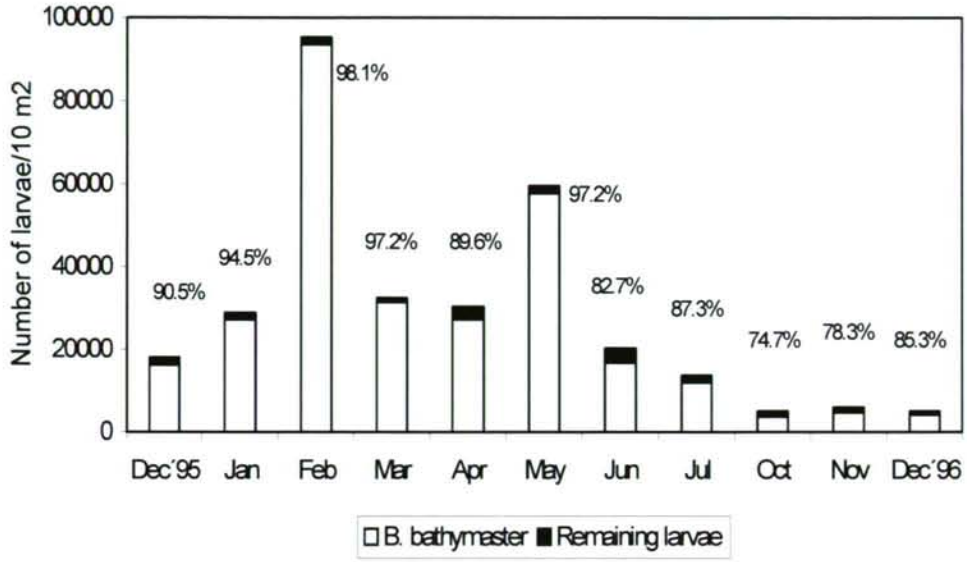


Figure 2. Total abundance of fish larvae and *Bregmaceros bathymaster* larvae. Percentages represent the *B. bathymaster* contribution to samples.

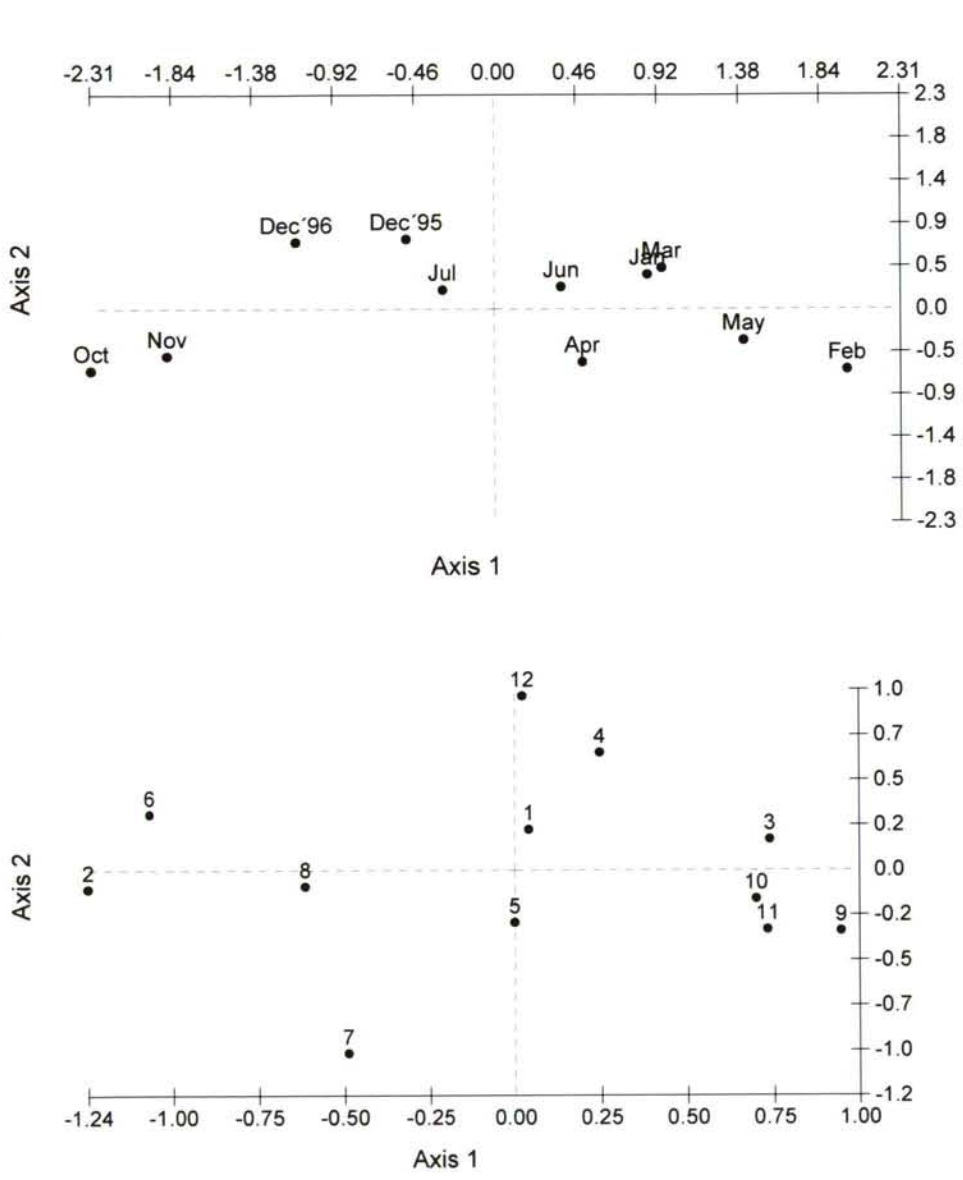


Figure 3. Ordination patterns (PCA) of sampling months (a) and sampling stations.

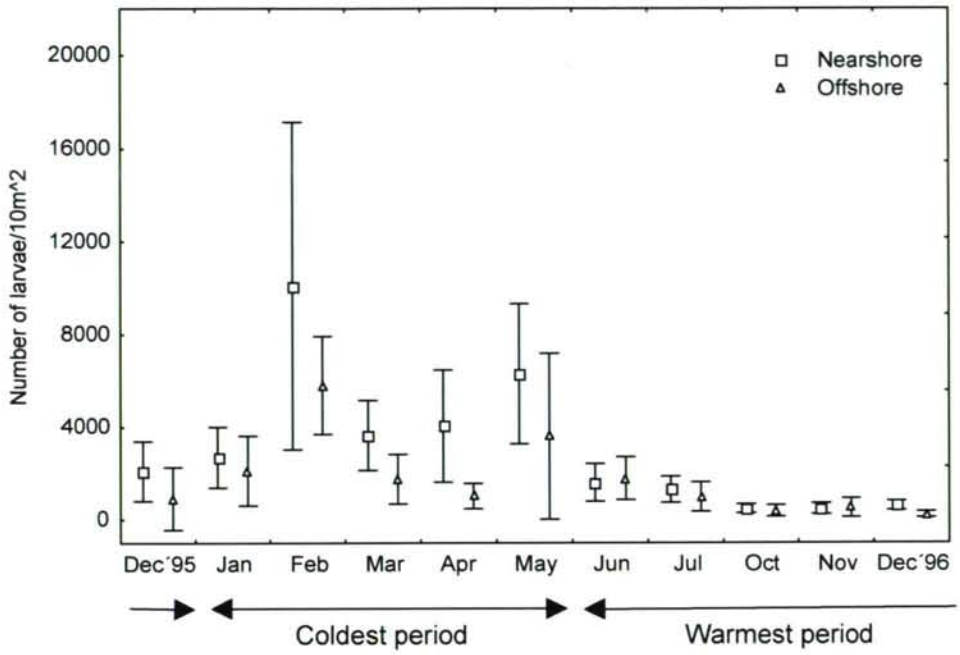
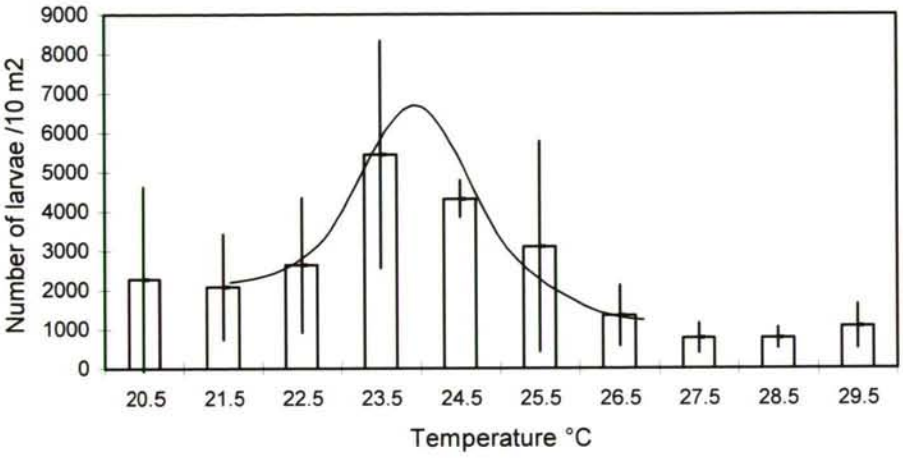


Figure 4. Mean values and 95% confident intervals (vertical lines) of the total fish larvae abundance; (a) nearshore stations (b) offshore stations.

a



b

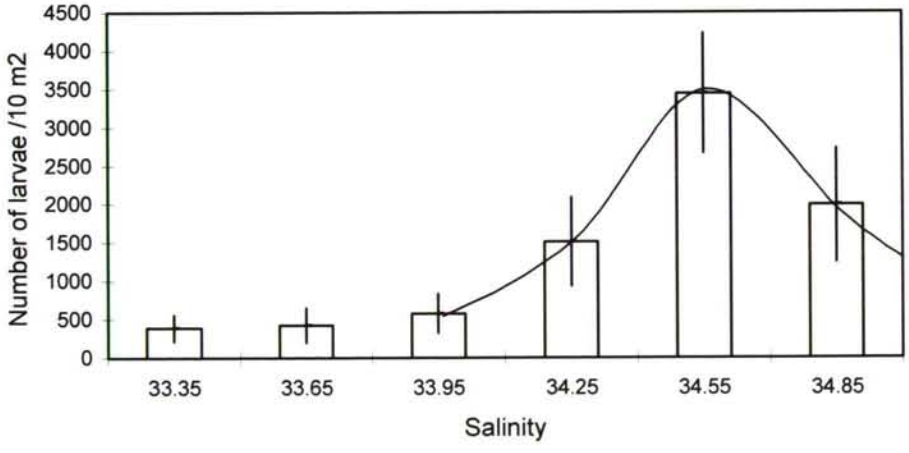


Figure 5. Relation between fish larvae abundance and environmental factors; (a) Temperature and (b) salinity.

4.4 Discussion

Only 1.18% of the fish larvae families collected in the surveyed area have a commercial value as adults, these are represented mainly by: Haemulidae, Lutjanidae, Carangidae, and Scombridae (Rojo-Vázquez and Ramírez-Rodríguez, 1997). They were relatively scarce in the area, and most of the fish larvae found represent commercially unimportant species. However, their ecological relevance should be considered as they are potential predators or food for other species, including those with commercial value (Horn, 1980). In this survey, sampling was performed considering that the nighttime fauna dwelling along 71% of the water column was being sampled. Nighttime ichthyoplankton has been recognized as being more diverse than that collected during daytime (Vásquez-Yeomans et al., 1998; Pitts, 1999). The absence of most of the main commercial species in our samples could be related, among other factors, to the sampling gear selectivity, since only the 0.5 mm net material was considered. Even the unusual dominance of *B. bathymaster*, which has been reported as the most important neritic ichthyoplankter in the Tropical Mexican Pacific (Acal, 1991; Ahlstrom, 1971; 1972) could have been underestimated by analyzing the 0.5 mm net only.

The fish larvae recorded herein are mostly epipelagic forms, with a tropical-subtropical distribution; this agrees with the general biogeographic affinities of the adult fish species reported in previous works in the same area (Aguilar-Palomino et al., 1996; Rojo-Vázquez

and Ramírez-Rodríguez, 1997), and in the adjacent Californian region (Ahlstrom, 1971, 1972). A qualitative comparison of the local ichthyoplankton composition with the adult ichthyofauna known to dwell in the Jalisco and Colima neritic zone yielded some interesting data. Out of 130 species recorded by Aguilar-Palomino et al. (1996), only 32 (24.6%) were found in our ichthyoplankton samples, whereas 15 (20%) out of 75 species recorded by Rojo-Vázquez and Ramírez-Rodríguez (1997) in the same zone, were collected as larvae in our survey. These results suggest that only a small portion of the resident adult populations dwelling in the area are represented as larval forms in the zooplankton. According to Ahlstrom (1972), fish larvae abundance is not necessarily proportional to adult abundance in the same zone. Several factors such as fecundity, the extent of time as a planktic stage, the temperature-development relation, mortality rates, spawning season, age, and even environmental and methodological factors can produce these differences.

Moser (1996) reported a total of 158 families and 586 species in the northeastern portion of the Pacific Ocean, including the Gulf of California. The ichthyoplanktonic fauna of this zone is much better known than that dwelling in the tropical section of the Mexican Pacific coast, in which only about 80 families and some 150 species have been reported (Franco-Gordo et al., 1999). All the species recorded in this study have been collected previously in the Mexican Tropical Pacific and adjacent zones (Ahlstrom, 1971, 1972; Acal, 1991). It is expected that faunistic records will increase as new surveys are

carried out in this tropical area, as predicted by Kendall and Matarese (1994).

Species of *Bregmaceros* are common and abundant forms, and as adults most of them can be collected in surface layers (Moser, 1996); however, due to their small size (ca. 12 cm), they are not attractive for fisheries, but have been described as ecologically relevant in the oceanic trophic webs (Zavala-García and Flores-Coto, 1994). *Bregmaceros bathymaster* is the most abundant fish larvae species in the Tropical Mexican Pacific, and Stevens and Moser (1996) described it as a common tropical-subtropical form. It is scarce at higher latitudes; in the California Current System it is ranked as species number 103 considering its overall relative abundance (Moser et al., 1993). Ahlstrom (1971, 1972) mentioned that this species was most abundant at stations near Mexico, although it represented only 1.6% of the total larvae numbers in his samples. The average abundance of this species in the surveyed area (295,036 org $10m^{-2}$) is several orders of magnitude over that estimated for bregmacerotids in the CC system (0.1 - 4.1 per $10m^{-2}$) by Moser et al. (1993), and probably represents the highest abundance ever reported for this species in the region. Despite this extraordinary larval abundance of *B. bathymaster*, always the main ichthyoplankter in our samples, the adults have not been reported in the area. This may be related to the life-cycle and life strategies of the species, including distinct migrational patterns, habitat preferences,

and environmental conditions of larval, juvenile, and adult stages (Loeb, 1986; Saucedo-Lozano et al., 1998).

Variations in zooplankton abundance can affect larval fish populations in several ways, and a positive correlation is expected when zooplankton is visualized as food for fish larvae (McGowan et al., 1996; Mullin and Cass-Clay, 1997). Zooplankton biomass was studied in the surveyed area (Franco-Gordo et al., submitted) and was found to behave as the ichthyoplankton in terms of space and time distribution. In this kind of interaction, a succession of species peaking at different times is expected (Skud, 1982), but this was not true for the surveyed community in which due to the year-round prevalence of *B. bathymaster*, there is no shift of dominance.

Our results show that *B. bathymaster* larvae tended to be more abundant coastwards, as was previously reported by Ahlstrom (1971, 1972) and later on by Stevens and Moser (1996). Being so overwhelmingly dominant in the surveyed area year-round, the nearshore habits of *B. bathymaster* larvae can explain most of the overall tendency of the fish larvae community to be denser in the coastal zones of the Mexican Pacific. Shoreward higher abundance of other relevant ichthyoplankters in the region has been reported by Lavenberg et al. (1986, 1987). Significant differences between nearshore and offshore larval abundances were found during the cold period. According to our hydrographic data and to the results of Filonov et al. (2000), during winter the study area is influenced by

advective processes generated by the presence of the California Current. Besides its influence in the local and regional production cycles, advective processes constitute an important larval transport mechanism (Pitts, 1999), the differential inshore-offshore distribution of *B. bathymaster* larvae, supports this idea.

Spawning grounds of fish are often distant from nursery areas (Norcross and Shaw, 1984), and apparently this is true for *B. bathymaster*. This species probably spawns in the ocean and its larvae are transported coastwards, with better possibilities to find nearshore environments with favorable conditions for development (Norcross and Shaw, 1984). This idea is supported by (1) the absence of adults in the neritic zone, (2) the increased general productivity along the coastal systems in this region (Mullin, 1986), and (3) the presence of several embayments along the surveyed area. These kind of environments have been described as nursery areas in other geographic regions (Lenanton, 1982; Vásquez-Yeomans, 1990; Vásquez-Yeomans and Richards, 1999). Recently, González-Armas et al. (1999) confirmed the importance of the surveyed area as a spawning ground for large pelagic fishes and other ecologically or fisheries-relevant species. The high abundance of *B. bathymaster*, recorded year-round in the surveyed area suggests that this species has a continuous breeding cycle, as suggested by Stevens and Moser (1996). However, the species abundance has moderate month-to-month and strong seasonal variations, as has been reported for other common fish species in

adjacent areas of the Eastern Pacific (Brewer and Smith, 1982; Macewicz and Hunter, 1993). The non-linear relation between environmental parameters and larval abundance agree with a unimodal model response, which states that organisms occurring in a characteristic, limited range of habitats, tend to be most abundant around their particular environmental optimum (ter Braak and Prentice, 1988).

The two abundance distribution patterns shown by the ichthyoplankton throughout the surveyed period seem to be related to the seasonal variation of the hydrographic regime in the region. The winter and spring season was characterized by the CC, with relatively richer waters, higher plankton biomass, and lowest water temperatures (Wyrtky, 1965; Pacheco-Sandoval, 1991; McGowan et al., 1996; Millán-Núñez et al., 1996; Godínez-Domínguez and González-Sansón, 1998, Filonov et al., 2000) seem to provide better conditions for increased fish reproduction rates. This was reflected by the highest larval abundance recorded during the colder months. Contrastingly, when the CC weakened during the summer and autumn period, the overall larval abundance, including that of *B. bathymaster*, decreased dramatically. This could be related to the influence of the oligotrophic tropical waters (North Equatorial Current) in the area during the warmest months of the year. A reproductive strategy of *B. bathymaster* to breed in the most favorable conditions for the survival of its early stages could be involved in the low overall ichthyoplankton density featuring this season. High winter and

reduced summer abundance values have been reported also for other zooplankton groups in the central Mexican Pacific (Sánchez-Osuna and Hendrickx, 1984; Jiménez and Suárez-Morales, 1998), and in other areas of the Eastern Tropical Pacific (Alvariño, 1980; Gasca and Suárez-Morales, 1992). High secondary productivity episodes in the CC System are episodic, spatially limited (McGowan et al., 1996; Brodeur et al., 1996). The high variability of abundance values in the surveyed area suggests this kind of episodic, localized processes enhancing the productivity in the area. Lucano-Ramírez (1999) and Santamaría-Miranda et al. (1995) stated that some of the commercially relevant species in the area show their reproductive season from November to April (winter). This could mean an increased potential food availability for their larvae. A coupling between the local productivity with the reproductive strategies of some of the most abundant fish species dwelling in the Mexican Tropical Pacific is suggested.

4.5 References

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Capítulo 5

Diversity of ichthyoplankton in the central Pacific: A seasonal survey

Franco-Gordo, C., Godínez-Domínguez E., Suárez-Morales, E., & Vásquez-Yeomans, L. (2003). *Estuarine Coastal Shelf Science*, 57, 111-121

DIVERSITY OF ICHTHYOPLANKTON IN THE CENTRAL MEXICAN PACIFIC: A SEASONAL SURVEY

Abstract

The seasonal variation in the diversity of ichthyoplankton was analyzed from samples collected monthly during a year cycle off the central Pacific coast of Mexico. Samples were collected using a Bongo net at 12 stations during 11 months, from December 1995 through December 1996. The most dominant species was *Bregmaceros bathymaster*, its relative density varied between 77 and 98%. Two main seasonal patterns were revealed the analyzing the dynamics of the coastal water mass and the ichthyoplankton assemblage ordination in relation to diversity. Diversity values (jack-knifed H = 0.24) were relatively low from January to May, and indicated a first seasonal pattern, related to a period dominated by the influence of the California Current, with surface temperatures ranging between 21 and 24°C. The second pattern was featured by diversity values five-fold higher than in the winter-spring (H = 0.92). These were related to the influence of warm, tropical waters from the Equatorial Countercurrent, with associated temperatures ranging between 26 and 29.2°C. A transitional period was identified in June and December; it represented a mixed assemblage and yielded the highest richness. Diversity null models were useful as tools to confirm the major seasonal patterns of the surveyed ichthyoplankton community.

Key words: Diversity, rarefaction, Shannon index, probability of interspecific encounter, fish larvae, null models, continental shelf.

5.1 Introduction

The interest in the fish larvae communities has increased noticeably during the last two decades as a tool to provide insights of the ecology and dynamics of marine zooplankton (Moser & Smith, 1993). These surveys have contributed to improve our knowledge on the ecological relations among the communities based on the analysis of the species composition and its time and space variability. These changes can be described objectively using statistical methods (Richards, McGowan, Leming, Lamkin, & Kelley,. 1993).

Ichthyoplankton surveys in tropical areas of the Eastern Tropical Pacific are still scarce (Acal, 1991; Ahlstrom 1971; 1972; Franco-Gordo, Flores-Vargas, Navarro-Rodríguez, Fúnes-Rodríguez, & Saldierna-Martínez, 1999; Loeb & Nichols, 1984; Loeb, Smith, & Moser, 1983; Moser, 1996), and most of them have restricted time coverage. Hence, smaller-scale or seasonal phenomena affecting the entire community are commonly lost or overlooked in an isolated, non-sequential survey.

Although its definition has been discussed for decades (Ludwig & Reynolds, 1988; Shannon & Weaver, 1963;), species diversity is one of the main ecological features of a community. There are several

indices available, combining the species richness and evenness, and giving insights on how are the abundance distributed among the species, and thus evaluate the distribution of the relevance attributed to each species (Ludwig & Reynolds, 1988). In the plankton communities, diversity is a valuable index which has been used to evaluate temporal or spatial variations in the species composition of the fish larvae. This is particularly relevant when a zone with a seasonal, highly variable hydrology is surveyed. Currently, it is a well-known fact that the surveyed area shows an hydroclimatic seasonality based on the regional patterns of oceanic circulation (see Filonov, Tereshechenko, Monzón, González-Ruelas & Gódínez-Domínguez, 2000; Wyrtki, 1965) and in the coastal dynamic processes. This seasonal pattern is related to productivity indicators such as zooplankton biomass (Franco-Gordo, Godínez-Domínguez, & Suárez-Morales, 2001a), and ichthyoplankton abundance (Franco-Gordo, Godínez-Domínguez, Suárez-Morales, & Flores-Vargas,2001b). In this work we hypothesize that temporal oceanographic processes are reflected in the ichthyoplankton community structure and we demonstrate that a species diversity analysis is sensitive enough to detect seasonal patterns.

5.2 Material and Methods

The area was surveyed using a 12 station plan (see Fig. 1 chapter 2) on board the BIP-V oceanographic vessel. Zooplankton trawls were performed monthly during nocturnal samplings (20:00 to 07:00 h)

from December 1995 through December 1996, no samplings were made in August and September 1996 because of adverse climatological conditions. Zooplankton trawls were performed following Smith & Richardson (1977). Samples were collected by means of a Bongo net with 0.505 mm mesh size. This gear was hauled obliquely within a 42-86 m depth, which implied a sampling range of 60-90% of the water column in the surveyed area, exclusively over the continental shelf. A digital flowmeter was adapted to the net mouth in order to estimate the amount of water filtered by the net. Samples were fixed and preserved in a 4% formalin solution buffered with sodium borate (Griffiths, Fleminger, & Vannucci, 1976). Temperature and salinity were measured at each station with a Seabird SBE-19 CTD profiler.

Monthly diversity was estimated using the normalized values (Larvae $10m^{-2}$, in accord to Smith & Richardson, 1977) by means of the Shannon-Weaver indices (H) (Peet, 1974; Shannon & Weaver, 1963). The accumulated values of the Shannon were used, following the criteria of Ludwig & Reynolds (1988), to explore the relation between sample size and diversity.

To explore statistically the possibility that diversity may vary in a temporal pattern, monthly average value of the Shannon indices were calculated using the Jack-knife sampling technique (Zahl, 1977), which allows a robust estimation of the confidence intervals of diversity. The method performs repeated estimations of H, omitting

from the calculation of a random sample. Each repetition generates a Jack-knife estimate, Vj_i, and the best estimated V value is the average of the VP.

$$VP_i = (nV) - [(n\text{-}1)(Vj_i)]$$

The confidence interval was calculated by estimating the standard error (SE):

$$\text{SE of } VP = var(VP) / n$$

where *var* is the variance of VP and n is the number of samples.

Calculations were made using the procedures described by Routledge (1980), and Heltshe & Forrester (1983). A one-way variance analysis was performed in order to determine monthly diversity differences; the values used are the Jack-knifed pseudovalues, which are assumed to be normal (Zahl, 1977).

A canonical correspondence analysis (CCA) was employed to determine the seasonality pattern of the larval fish assemblage. Data were pooled by months on the basis of abundance values and the environmental variables were temperature at the depth of 10 m, dissolved oxygen and salinity. A Monte Carlo permutation test was employed to determine the statistical significance of the relation

between the species and the whole set of environmental variables (ter Braak & Smilauer, 1998)

In order to compare the diversity between ecological-oceanographic periods found by means of the diversity and assemblage analysis, two null models (Gotelli & Entsminger 1999) were used. In both cases the calculus procedure employed repeated 1000 times the abundance level with Monte Carlo method to generate a mean and a variance of richness and evenness.

1. A rarefaction analysis was carried out to compare the expected richness between diversity periods. Rarefaction curves (Sanders, 1968) are frequently used to compare species richness between samples with different abundance Simberloff (1972).
2. The Hurlbert´s PIE (Hurlbert 1971) was used to measure evenness. This index calculates the probability that two randomly sampled individuals from the assemblage represent two different species (Gotelli & Graves 1996).

$$PIE = (N / N\text{-}1)\left(1 - \sum_{i=1}^{S} (m_i / n)^2\right)$$

where N is the total number of individuals in the collection, S is the total number of species in the collection, m_i is the number of individuals of species i in the collection, and n is the number of individuals in the subsample.

5.3 Results

A well-defined mass of water structure composed by two hydroclimatic periods was found (Fig. 1). Temperature profiles from CTD data, during July are representative of tropical oceanographic conditions, with warm surface waters SST (29.7 °C) and strong stratification with deep thermocline. March profiles featured contrasting conditions, with a thicker mixing layer and a lower SST (22 °C). The thermocline is close to the surface and vertical profiles means the existence of located and episodic advective process (in accord to Franco-Gordo et al. 2001a,b). Coastal upwelling is produced by wind stress from the NW, which displaced water offshore and replaces it with nutrient-rich, deeper cold water.

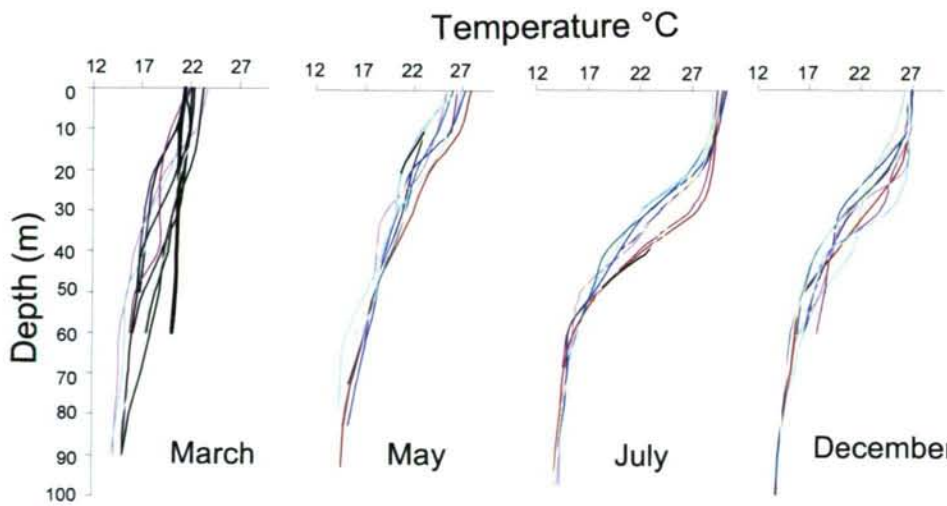

Figure 1. Temperature profiles ilustrating the seasonal variation of the coast water mass structure.

The December profiles are indicative of the end of the tropical season, and the end of the influence of CC is indicated by the temperature profiles of May, with increasing SST values and a deeper thermocline. Both salinity and temperature at 10 m showed variations throughout the year (Fig. 2). Salinity was stable between December 1995 and June 1996 with monthly average values within a range of 34.2-34.7. Temperature showed two a period representative cycle in this sense patterns, with a colder period, between January and May, with March being the coldest (21.4°C) month, and warm period during summertime (July-December), which was featured by the highest temperature averages, and varied within the 26-29°C range. This result coincides with the local oceanographic seasonal pattern proposed for the study area by Filonov et al., (2000) and in general with the large scale oceanic surface currents (Wyrtki, 1965).

During the 11 cruises a total of 111 taxa were recorded. A total a 111 taxa include 57 families and 81 genera (see Franco-Gordo 2001). The most abundant and frequent species was *Bregmaceros bathymaster*, followed by *Dormitator latifrons* and *Harengula thrissina*. Although a succession of not abundant species was recorded throughout the survey, their relative abundance was determined for each period (Table 1).

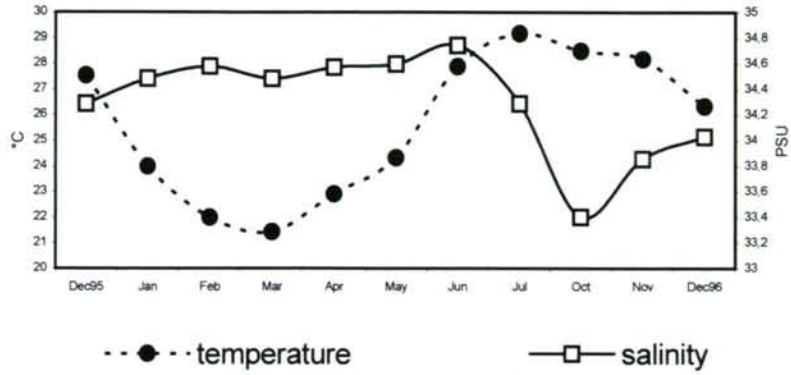

Figure 2. Monthly average of temperature and salinity (sampling sites) recorded at 10m depth.

Accumulated diversity values show that December 1995, April, and June diversity (H) and species richness (S) are stabilized (Fig. 3), with the same number of accumulated samples, and with accumulative density values of 27581, 27882, and 19033, respectively. During January, July, and December 1996, diversity (H) was relatively stable, but species richness did not reach an asymptotical value sequence in any of these cruises. On the other hand, species richness and diversity stabilized again in different accumulated samples during February and May only. March, October, and November did not show an asymptotic behavior in the 12 samples. This reveals that the sampling sizes necessary to evaluate diversity and species richness differ in most cases and has month-to-month variation. This should be considered in further sampling efforts. A high correlation ($r^2 = 0.82$) was found between the Jack-knifed monthly diversity (H) of the fish larvae species and temperature of the water (Fig. 4).

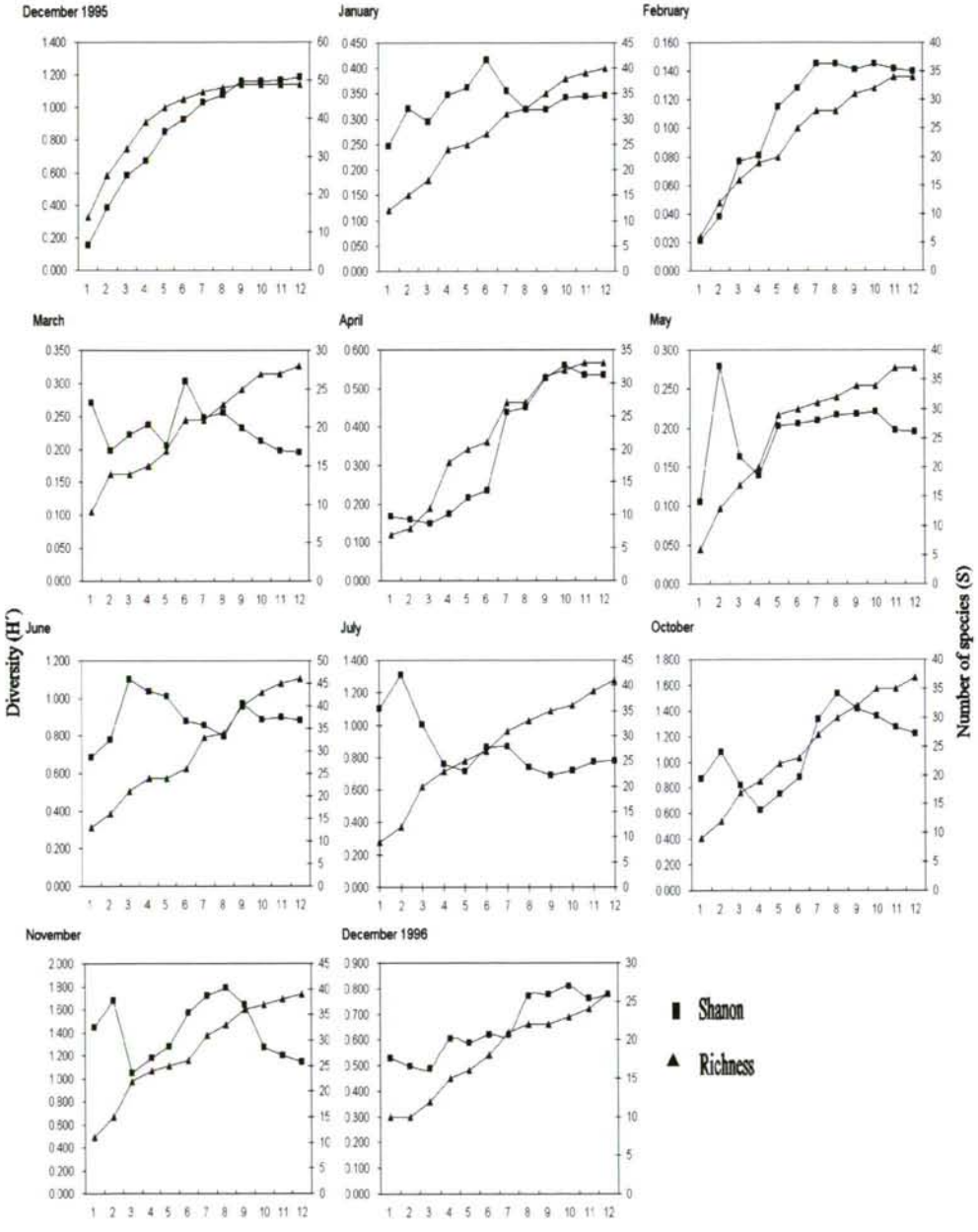

Fig. 3. Accumulated distribution of the diversity indices of the ichthyoplaknton community of the central Mexican Pacific.

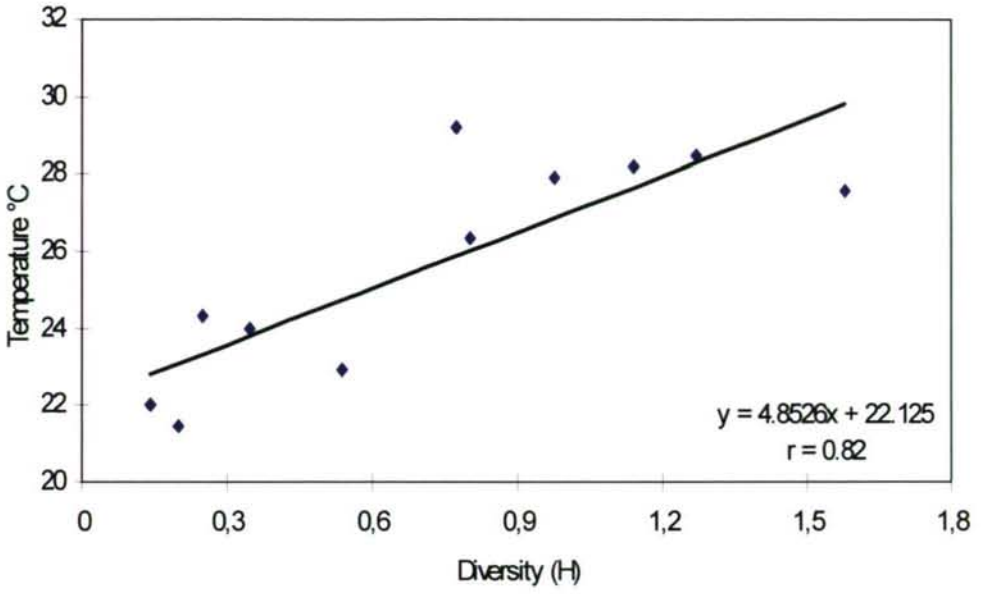

Figure 4. Relation between Shannon diversity and temperature (10m depth)

The canonical ordination of the months defined three main periods, where the period from January to May represent the influence of CC, the second period (July to November), represent the tropical affinity season, and a third one (June, and both December months 1995 and 1996) represent the transition between seasons (Fig. 5). A high inter-set correlation (0.78) between temperature and the first axis, allowed to recognize temperature as the main factor inducing the temporal ordination. The permutation test ($P < 0.01$) shows that the relation between the species and the environmental variables is highly significant.

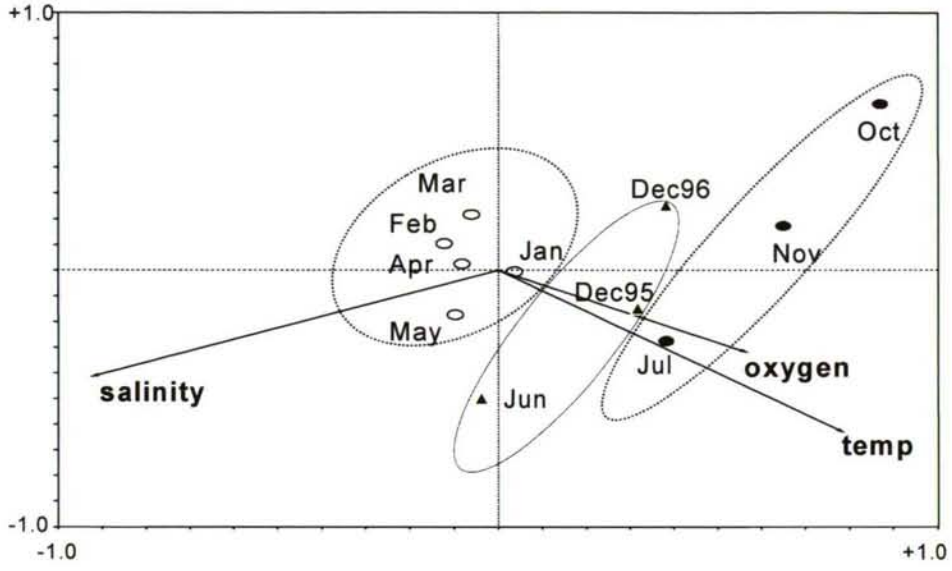

Figure 5. Ordination of ichthyoplankton assemblajes by months.

Jack-knifed diversity values (Fig. 6) showed monthly variations ($F = 8.28$, $P < 0.05$); diversity varied during the year between 0.13 (February), and 1.58 (December 1995). A multiple ranges test was unable to determine coherent seasonal groups, so data was pooled in accord to canonical ordination periods. Highest Jack-knifed values ($H = 0.92$) were recorded from July through November 1996. During the transition phase diversity was $H = 0.7$ and lowest diversity values ($H = 0.24$) were those recorded between January and May ($P < 0.01$).

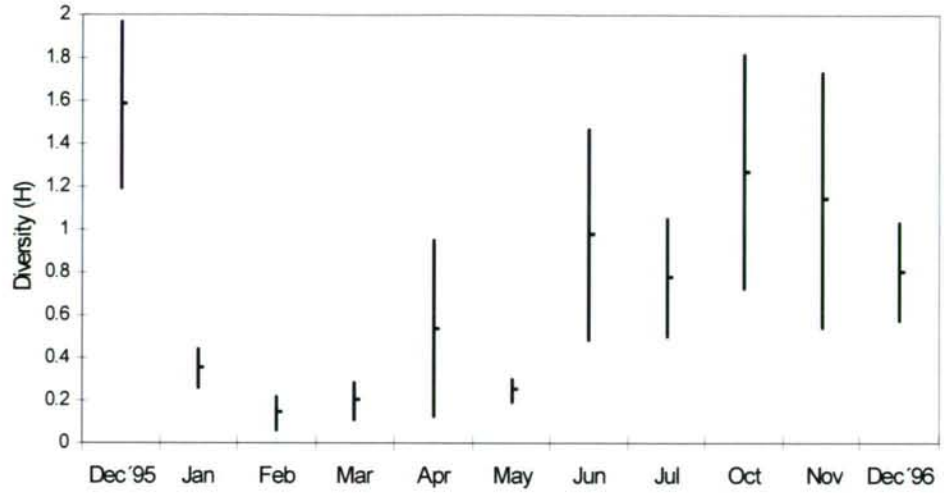

Figure 6. Mean diversity Shannon estimated with Jack-knife procedure Vertical lines represent 95% confident intervals.

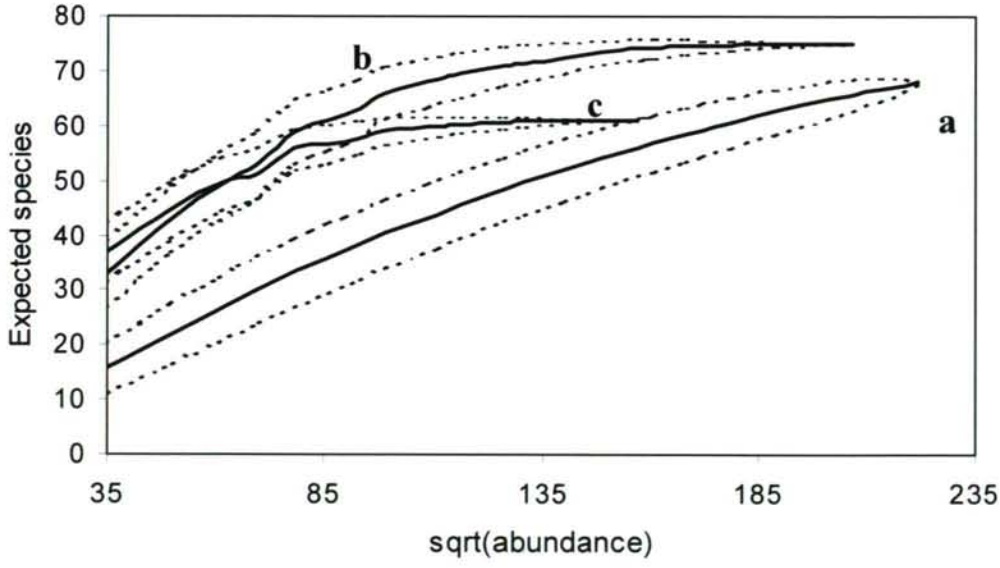

Figure 7. Rarefaction curves for fish assemblages in the Central Mexican Pacific.(a) California Current period, (b) transitional period, and (c) tropical period.

In order to analyze seasonal diversity patterns, samples from January to May, July to November, and June and December (both, 1995 and 1996) were pooled in three sampling periods: the CC, the tropical, and the transitional period, respectively. During the transitional period the species number was highest (75). During the CC period the species richness was significantly higher (68 taxa) than in the tropical period (61 taxa) according to the rarefaction curves (Fig. 7). The Hurlbert's PIE showed the highest probability of interspecific encounter during the tropical period (Fig. 8). Due to non-overlapping confidence intervals in both cases between the tropical and CC periods, a statistic test to compare differences was not considered necessary.

Figure 8. Probability of and interespecific encounter PIE from (a) California Current period, (b) transitional period, and (c) tropical period.

Table 1 Relative abundance of fish larvae during the main hydroclimatic periods in the Mexican tropical Pacific Ocean.

	Taxa	larvae/10m^2	Positive hauls	Abundance (larvae/10m^2) Cold period [1]	Transition period [2]	Warm period
1	*Bregmaceros bathymaster*	295036	132	237226	37395	20415
2	*Dormitator latifrons*	3484	110	2031	732	721
3	Sciaenidae	2178	65	1513	355	310
4	*Harengula thrissina*	1736	21	395	1341	0
5	Engraulidae	1728	36	1287	223	218
6	*Gobionellus* sp.	1098	65	485	420	193
7	*Vinciguerria lucetia*	909	57	224	567	118
8	*Euthynus lineatus*	660	37	25	153	482
9	*Benthosema panamense*	470	34	265	133	72
10	*Symphurus elongatus*	363	24	348	0	15
11	Gobidae type A	349	41	166	95	88
12	*Opistonema* sp.	333	19	259	69	5
13	*Cetengraulis mysticetus*	301	12	301	0	0
14	*Auxis* sp.	277	20	102	108	67
15	Eloetridae	273	14	52	157	64
16	*Syacium ovale*	267	37	48	97	122
17	Pomacentridae	226	17	18	105	103
18	*Sphoeroides annulatus*	190	12	10	41	139
19	*Symphurus chabanaudi*	165	15	63	45	57
20	*Xyrichtys* sp.	164	27	61	28	75
21	*Caranx caballus*	130	18	4	66	60
22	*Abudefduf troschelli*	121	14	22	48	51
23	Gobidae type C	117	7	0	0	117
24	*Labrisomus multiporosus*	116	8	110	6	0
25	*Eucinostonus enthomelas*	108	9	26	56	26
26	*Balistes polylepis*	104	15	5	52	47
27	*Caranx sexfasciatus*	102	13	12	27	63
28	*Chloroscombrus orqueta*	99	14	19	72	8
29	Haemulidae	91	11	40	41	10
30	*Scorpaena* sp.	91	10	77	10	4
31	*Lutjanus novemfaciatus*	89	5	0	5	84
32	*Sphyraena ensis*	88	9	9	15	64
33	*Synodus sechurae*	87	12	40	29	18
34	*Thalassoma* sp.	77	8	0	56	21
35	*Etropus crossotus*	71	14	27	18	26
36	*Porichthys margaritatus*	69	7	3	0	66
37	*Halichoeres dispilus*	65	12	31	21	13
38	*Psenes sio*	54	4	22	32	0
39	*Symphurus atramentatus*	53	9	28	19	6
40	*Bathycongrus macrurus*	52	9	42	0	10
41	Moringuidae	51	9	37	8	6
42	Labrisomidae	51	4	47	4	0
43	*Cubiceps pauciradiatus*	50	7	0	5	45
44	*Pontinus* sp.	48	7	40	5	3
45	*Gobiesox* sp.	44	2	0	27	17
46	Gobidae type B	42	6	8	0	34
47	*Lutjanus guttatus*	41	6	10	21	10
48	*Eucinostomus gracilis*	35	6	10	25	0
49	*Ophidion* sp.	35	6	30	0	5
50	*Sphyraena* sp.	30	3	0	30	0

continued on next page

Table 1. Continued

Taxa	larvae/10m²	Positive hauls	Abundance (larvae/10m²) Cold period [1]	Transition period [2]	Warm period
51 *Ophichtus* sp.	30	5	24	0	6
52 Gobioesosidae	29	3	0	29	0
53 Scorpaenidae	27	1	0	27	0
54 Apogonidae	27	2	0	0	27
55 *Decapterus* sp.	22	3	0	22	0
56 *Elops affinis*	21	4	15	6	0
57 *Bhotus leopardinus*	21	3	15	0	6
58 *Mugil cephalus*	20	5	12	4	4
59 *Scorpaennodes xyris*	20	5	13	5	2
60 *Hemiramphus saltador*	20	2	0	0	20
61 *Apogon retrosella*	18	4	5	4	9
62 *Citharichthys platophrys*	16	4	16	0	0
63 *Lutjanus argentiventris*	14	3	0	10	4
64 *Selene brevoortii*	13	3	0	3	10
65 *Paralichchys woolmani*	13	3	10	3	0
66 *Paraconger nitens*	12	2	12	0	0
67 *Halichoeres semicinctus*	11	2	0	11	0
68 Ophidiidae	11	2	11	0	0
69 *Engyophrys sanctilaurentia*	11	1	11	0	0
70 *Psenes pellucidos*	11	2	11	0	0
71 *Myrophis vafer*	10	2	4	6	0
72 *Hypsoblennius* sp.	10	2	0	0	10
73 *Serranus* sp.	9	2	4	5	0
74 *Diaphus pacificus*	8	2	0	8	0
75 *Symphurus williamsi*	7	2	0	0	7
76 Symphurus type B	6	1	0	6	0
77 *Albula* sp.	6	1	0	6	0
78 Mictophidae	6	1	6	0	0
79 *Lephophidium negropina*	6	1	6	0	0
80 Symphurus type D	6	1	6	0	0
81 Symphurus type C	6	1	6	0	0
82 *Anthenarius sanguineus*	6	1	0	0	6
83 *Lampanyctus parvicauda*	6	1	0	6	0
84 *Fistularia cometa*	6	1	0	5	1
85 *Cheilopogon heterurus hubbsi*	6	1	0	0	6
86 *Opistognatus* sp.	6	1	0	6	0
87 Labridae	5	1	0	5	0
88 *Stegastes rectifraenum*	5	1	0	5	0
89 *Ammodytoides* sp.	5	1	0	5	0
90 Kiposidae	5	1	5	0	0
91 Hemiramphidae	5	1	5	0	0
92 Melanostomiidae	5	1	5	0	0
93 *Paraconger californiensis*	5	1	5	0	0
94 Balistidae	5	1	0	5	0
95 *Melanocetus johnsoni*	5	1	0	0	5
96 *Hyporhampus rosae*	5	1	0	0	5
97 *Lestidiops neles*	5	1	0	0	5
98 Ophichtidae	5	1	0	0	5
99 Priacantidae	5	1	0	0	5
100 *Parantias colonus*	5	1	0	0	5
101 *Gymnothorax* sp.	4	1	0	4	0
102 *Bollmania* sp.	4	1	0	4	0
103 Tetraodontidae	4	1	4	0	0
104 *Antherionella nepenthe*	4	1	4	0	0
105 *Trachinotus kennedyi*	4	1	0	4	0
106 Dactiloscopidae	3	1	0	3	0
107 *Bathylagus wesethi*	3	1	0	3	0
108 *Entomacrodos chiostictus*	3	1	0	3	0
109 *Pseudograma thaumasium*	3	1	0	3	0
110 Bramidae	3	1	0	3	0
111 *Encheliophis dubis*	3	1	0	0	3

*Cold period January to May (California Current period)

*Warm period July, October and November (tropical period)

*Transitional period June and December

5.4 Discussion

Diversity is a combination of species richness and evenness; however, in some cases the number alone might be misleading. This is because the same diversity index value can be obtained from a community with low evenness and high richness and vice versa (Ludwig & Reynolds, 1988). Hence, evaluation of the relevance of each factor was necessary to assess a reliable diversity level for our ichthyoplankton community.

Monthly values of jack-knifed diversity (H) oscillated between 0.16 and 1.58, with an overall diversity of 0.723. This is a relatively low value, but it is similar to that reported by Acal (1991) for fish larvae in a survey of the Central Mexican Pacific. Clearly, our low diversity values are related to the year-round high dominance of *B. bathymaster* in the surveyed area. According to Acal (1991) and to Ahlstrom (1971, 1972), *B. bathymaster* is one of the most dominant species in the Eastern Tropical Pacific. However, it is scarse at higher latitudes; in the CC system it ranks 103 for the overall abundance and 133 for the frequency in this area (Moser et al., 1994).

According to Magurran (1988) the minimum sample size for an estimation of species richness and diversity of a given community is variable. This was found to be true for some of our samplings since in some cases the accumulated diversity was stabilized but the

accumulated species richness was not. However, when diversity and species richness stabilize at the end of the curve, it indicates a reliable diversity level of the ichthyoplanktonic community in the surveyed area. This occurred during December, June, and April. Apparently, the minimum sample size for species richness was higher in five cruises than that required for diversity estimations. In other 3 cruises both factors reached and asymptotic stage with the same number of accumulated samples. Only in 3 cruises the sample size seemed to be insufficient to ensure representativity of the diversity, and species richness values. Despite this flaw, it suggests that in general terms the sampling effort seems to be adequate to support the ecological interpretations derived from our data set.

The highest diversity (H) values were recorded during the tropical period, when coastal flows run northwards. This flow is originated by the effect of a branch of the Northequatorial Current (Badan, 1997; Burkov, 1972; De la Lanza, 1991). It transports tropical, oligotrophic waters with a more speciose associated planktonic fauna (Gasca & Suárez-Morales, 1992; Hernández-Trujillo, 1998). This generates an important input of tropical species groups into the surveyed area, decreasing abundance, increasing the evenness and favoring higher diversity values. Apparently, this recomposition model is not completely coincident with our results. There is a clear local decrease of zooplankton biomass (Franco-Gordo et al., 2001a) and of fish larvae abundance (Franco-Gordo et al., 2001b) during the peak tropical influence; however, there was no evidence that the species

richness increased due to the warm water intrusion. The sampling net selectivity could have some influence in our results, discarding the smallest fraction, since only the 0.5 mm net material was considered. In spite of this, our sampling coverage of the water column and the fact that night samples were performed when the vertical migration patterns allowed higher possibilities of capture in surface layers (Lyczkowski-Shultz & Steen, 1991). This is why we speculate that stratification of the water mass could affect the recomposition pattern of the local ichthyoplankton fauna. Furthermore, Franco-Gordo et al. (2002) determined, during this period, a clear offshore-inshore spatial segregation. This is why the transportation of oceanic larvae and the lack of oceanic samples could prevent us from capturing more species, mainly oceanic forms. The transitional period could be featured by having the highest species richness, probably as a result of mixing of tropical and subtropical (CC) species.

Lowest diversity values were related to the period during which the relatively richer California Current flows along this coast (Wyrtky, 1965). This colder, relatively more productive water moving southward from higher latitudes. Despite the fact that these conditions produce decreases in diversity and allow the dominance of one or a few species, the richness is higher than during the tropical period. This effect could be due to complexity of the coastal oceanography, with the influence of advective processes and wind stress, which would effect an inshorewards larval transport, most relevant during the CC period (Franco Gordo et al., 2001a,b). Some authors suggest

that besides transport, the distributional and recomposition patterns of ichthyoplankton assemblages are determined by the migrational behaviour of reproductive adults and by the ontogenic behavioural patterns of certain species (Gray, 1993; Harris, Cyrus, & Beckley, 1999; Leis, 1991). However, the fact that the lowest diversity season is also that with the highest species richness is one of the failures attributed to the diversity indices. Hence, several authors recommend analyze both richness and evenness in a separately analysis trying to find clear community patterns. The use of null models to estimate non-biological effect of sample size in richness and species evenness is highly recommended (Gotelli & Graves, 1996). We speculate that the efficiency of the Shannon Index is limited when used as a tool to explore the time variability of diversity.

The number of families recorded in the surveyed area (57) is much lower than that reported by Moser (1996) for the entire CC system (168) from plankton collections between 1951 and 1994. However, the number of families recorded by us is comparable to that recorded by Loeb et al. (1983) in the same region and during a single annual cycle (45). It is noteworthy to mention that they analyzed 1504 samples, 132 obtained in our sampling; this difference is indicative of a very high richness of ichthyoplankton in the Mexican Tropical Pacific area (Table 2).

Table 2. Species diversity and methological details of the ichthyoplanktonic works realized in the Mexican tropical Pacific area.

Source	Geographic coverage	Period	Methods	Depth and trawl	Number of samplings	Number of larvae	Families	Genera	Species
Loeb et al. 1983	CalCOFI net; from Oregon to Baja California. Oceanic stations	year cycle 1975	CalCOFI net device 1 m of mouth diameter. 0.50 mm and 0.33 mm meshsize both night and day	Oblique 0-200 m	1504	?	45	50	104
Ahlstrom, 1971	ESTROPAC I, tropical eastern Pacific; from 20N to 20S, coastal and oceanic stations	February and March 1967	1 m of mouth diameter. 0.50 mm and 0.33 mm meshsize both night and day	Oblique 0-200 m surface samplings	482	95109	54	74	89
Ahlstrom, 1972	EASTROPAC II, tropical eastern Pacific, from 20N to 15S, coastal oceanic stations	August and September 1967	1 m of mouth diameter. 0.50 mm and 0.33 mm meshsize samplings both night and day	Oblique 0-200 m	355	123185	82	105	113
Acal, 1991	From Mazatlán (México) to Acapulco, coastal and oceanic stations	April 1981	CalCOFI net device 1 m of mouth diameter. 0.50 mm meshsize (night and day)	Oblique 0-200 m	45	353	40	27	129*
Moser, 1996	CalCOFI net; from Oregon to Baja California. Oceanic stations	1951 -1994	CaLCOFI net device 1 m of mouth diameter. 0.50 mm and 0.33 mm meshsize samplings both night and day. Neustonic net	Neustonic Oblique 0-210 m	33.876 oblique 4.859 neustonic	13.6 millions	168	418	586
Franco-Gordo, 2001	Jalisco and Colima (México), coastal continental shelf	semimonthly from December 1995 to December 1996	Bongo net, 0.6 diameter 0.50 mm meshsize nocturnal samplings	Oblique (0-86 m)	132	63342	57	81	74

* The author named species, but in reality they are taxa

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Capítulo 6

Larval fish assemblages in waters off the central Pacific coast of Mexico.

Franco-Gordo, C. Godínez-Domínguez, E. & Suárez-Morales, E. (2002). *Journal of Plankton Research*. 24 (8), 775-784.

LARVAL FISH ASSEMBLAGES IN COASTAL WATERS OF THE CENTRAL PACIFIC OF MEXICO

Abstract

Spatial and seasonal variation of the ichthyoplankton assemblages was analyzed using monthly samples collected monthly during a 1 year cycle off the central Pacific coast of Mexico. Zooplankton samples were collected at 12 stations during 11 months, from December 1995 through December 1996. The analysis of coastal oceanographic conditions revealed two main seasonal patterns, one related to the California Current influence and the other a tropical one. A temporal recomposition of the ichthyoplankton assemblages was found to be related to each oceanographic pattern. During the California Current period (January- May) the larval fish assemblage was represented mainly by *Auxis sp.*, *Bentosema panamense*, *Cetengraulis mysticetus*, *Opistonema sp.*, *Symphurus elongatus*, *Gobionellus sp.*, *Dormitator latifrons*, *Bregmaceros bathymaster*. The tropical season assemblage (July, October, and November) was represented by *Harengula thrissina*, *Eutinnus lineatus*, *Vinciguerria lucetia*, *Syacium ovale*, and representatives of Eleotridae and Pomacentridae. An inshore-offshore gradient was observed during the tropical oceanographic periods, with a thermic stratification of the

water column over the shelf. Conversely, during the CC period, with coastal advective processes, the fish larvae assemblages were more homogeneous. Although a mixed, richer faunistic composition was expected in this transitional area, the overall biogeographic affinity of the surveyed community remained stable even in contrasting conditions.

Key words; zooplankton, ichthyoplankton, temporal and spatial patterns, advective process, Eastern tropical Pacific.

6.1 Introduction

Several environmental factors affect the survival and distribution of fishes at early developmental stages. Some of these factors include: local hydrographic conditions, associated transport processes, seasonal variability, density of preys and predators, and the spawning patterns of adult fishes (Gray, 1993). Along the northeast Pacific, reproductive strategies of coastal fishes exhibit a geographical pattern which seems to be correlated to the general ocean flow characteristics; offshore spawning of shelf species corresponds to periods of wind-driven inshoreward surface flow, thus retaining buoyant eggs and larvae within the coastal-neritic zone (Parrish et al., 1981). Dynamic events in the coastal ocean are represented by significant advective forces which are often of relatively short duration. Hence, it is interesting to examine the response of ichthyoplankton communities to local circulation processes mainly because of the considerable influence that short-term hydrodynamic

variability may have on the overall larval dispersal (Smith et al., 1999; Gray, 1996).

The ichthyoplankton composition of the Mexican central Pacific has been examined in several studies (Ahlstrom, 1971; 1972, Acal, 1991; González-Armas et al., 1993; Franco-Gordo et al., 1999). The community is represented by more than 50 families and approximately 150 species (Franco-Gordo, 2001). Abundance shows seasonal changes throughout the year (Franco-Gordo et al., 2001). However, the response of neritic ichthyoplankton assemblages to changes of the coastal hydrographic conditions, and their relation with the inshore-offshore gradient has not been examined in this tropical area. This survey analyzes the seasonal variability of the larval assemblages in relation to the oceanographic dynamics and to the inshore-offshore gradient in the Eastern tropical Pacific.

6.2 Material and Methods

The sampling grid included 12 stations (see Fig. 1 chapter 2). Zooplankton samples were collected monthly from December 1995 through December 1996, on board the BIP-V oceanographic vessel. August and September 1996 were not sampled because of adverse climatic conditions. Samples were obtained using a Bongo net with mesh sizes of 0.5 and 0.33 mm, only the 0.5 mm net was analyzed. Plankton hauls were oblique, from a depth of 42-86 m to the surface at each station, all of them over the continental shelf. Zooplankton

hauls were performed during nighttime (20:00-07:00 h) only. A digital flowmeter was adapted to the net mouth in order to estimate the amount of water filtered (Smith and Richardson, 1977). Samples were fixed and preserved in a 4% formaline solution buffered with sodium borate (Griffiths et al., 1976). Temperature and salinity were measured at each station with a Seabird CB19 CTD profiler. During January and February the environmental records were not realized simultaneously with the plankton samplings, and measurements made during previous days were considered for the general oceanographic characterization analysis, but these complementary data were not considered in the multivariate analysis.

Fish larvae were sorted out from the 132 original zooplankton samples collected with the 0.5 mm net plankton during the 11 sampling cruises. Abundance data were standardized into number of larvae under 10 square meters (Smith and Richardson, 1977). With these values a data matrix was built in order to perform the statistical analysis.

A canonical correspondence analysis (CCA) (ter Braak and Smilauer, 1998) was used to analyze the spatial structure of the larval assemblages, except during January and February when a detrended correspondence analysis (DCA) was performed due to the lack of adequate environmental data. To determine the temporal structure of the larval assemblages a CCA was performed using the cumulative samples by month; we used only those species that together

represented up to 98 % of the percentual cumulative frequency for the entire period. A Monte Carlo permutation test was used to determine the statistical significance of the relation between species and the entire set of environmental variables (ter Braak and Smilauer, 1998).

6.3 Results

6.3.1 Oceanographic patterns

Salinity and temperature of water at 10 m showed variations throughout the surveyed period (Table I). Salinity was stable between December 1995 and June 1996 with monthly average values ranging from 34.2 to 34.7 PSS (Practical Salinity Scale). Salinity decreased during the rainy season, with a minimum (33.4) in October. Relatively low temperature values characterized a cold season from January to May, March being the coldest month (21.4°C). Another thermic period was featured by higher temperature averages (26.3 to 29.2 °C), it included summer and autumn. Temperature profiles (Fig. 1) during July are representative of tropical oceanographic conditions, with warm surface waters (29.7 ºC SST), a strong stratification, and a deep thermocline. March profiles featured contrasting conditions, with a thicker mixing layer, and a lower SST (22.2 ºC). These conditions are related to the influence of the CC. During this cold season, coastal upwelling is produced by stress winds from the NW, which moves water offshore and replaces it with nutrient-rich, deeper cold water. The December profile is indicative of the end of the tropical

season in the area, during which the influence of the North Equatorial Current weakens and the progressive onset of the CC conditions is more evident (see Wyrtky, 1965). The end of the influence of the CC in the area is indicated by the thermic profile of May, with increasing SST values and a deeper thermocline.

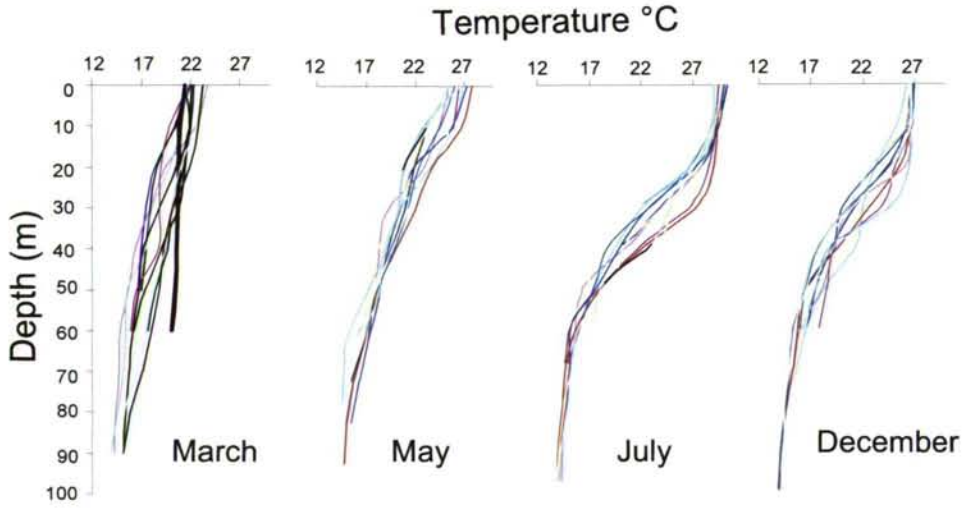

Figure 1. Temperature profiles characteristic of the oceanographic seasonality of coastal Mexican Tropical waters.

Table I: Monthly results for average temperature, salinity and disolved oxygen.

Month	Temperature (°C)	Salinity (ups)	Disolved oxigen (ml/l)
December 1995	27.54	34.26	4.72
January 1996	25.20	34.40	4.50
February 1996	23.80	34.40	4.60
March 1996	21.39	34.48	4.15
Aoril 1996	22.80	34.57	4.55
May 1996	24.33	34.59	5.00
June 1996	27.88	34.74	5.22
July 1996	29.17	34.28	5.22
October 1996	28.49	33.40	3.72
November 1996	28.17	33.85	5.03
December 1996	26.34	34.99	4.84

6.3.2 Larval fish assemblages

A total of 63,342 (314,357 larvae $10m^{-2}$) fish larvae were sorted from all zooplankton samples. The taxonomic analysis of the larvae yielded 54 families and 111 lower taxa . *Bregmaceros bathymaster* was the most abundant species during the entire survey (295 036 larvae $10m^{-2}$), followed by *Dormitator latifrons* (3 484 larvae$10m^{-2}$) and species of Sciaenidae (2 178 larvae$10m^{-2}$). The 17 most abundant taxa represented over 98% of the total larval numbers during the surveyed period (Table II).

Table II: Relative abundance of fish larvae during main hydroclimatic periods in the Mexican tropical Pacific.

				Number of larvae		
Taxa	key	Organisms $10m^{-2}$	positive hauls	cold period	transition period	warm period
1 Bregmaceros bathymaster	Brebat	295036	132	237226	37395	20415
2 Dormitator latifrons	Dorlat	3484	110	2031	732	721
3 Sciaenidae	Sciaen	2178	65	1513	355	310
4 Harengula thrissina	Hartrh	1736	21	395	1341	0
5 Engraulidae	Engrau	1728	36	1287	223	218
6 Gobionellus sp.	Gobsp	1098	65	485	420	193
7 Vinciguerria lucetia	Vinluc	909	57	224	567	118
8 Euthynus lineatus	Eutlin	660	37	25	153	482
9 Benthosema panamense	Benpan	470	34	265	133	72
10 Symphurus elongatus	Symelo	363	24	348	0	15
11 Gobidae A	GobtiA	349	41	166	95	88
12 Opistonema sp.	Opisp	333	19	259	69	5
13 Cetengraulis mysticetus	Cetmys	301	12	301	0	0
14 Auxis sp.	Auxsp	277	20	102	108	67
15 Eloetridae	Eloetr	273	14	52	157	64
16 Syacium ovale	Syaova	267	37	48	97	122
17 Pomacentridae	Pomace	226	17	18	105	103

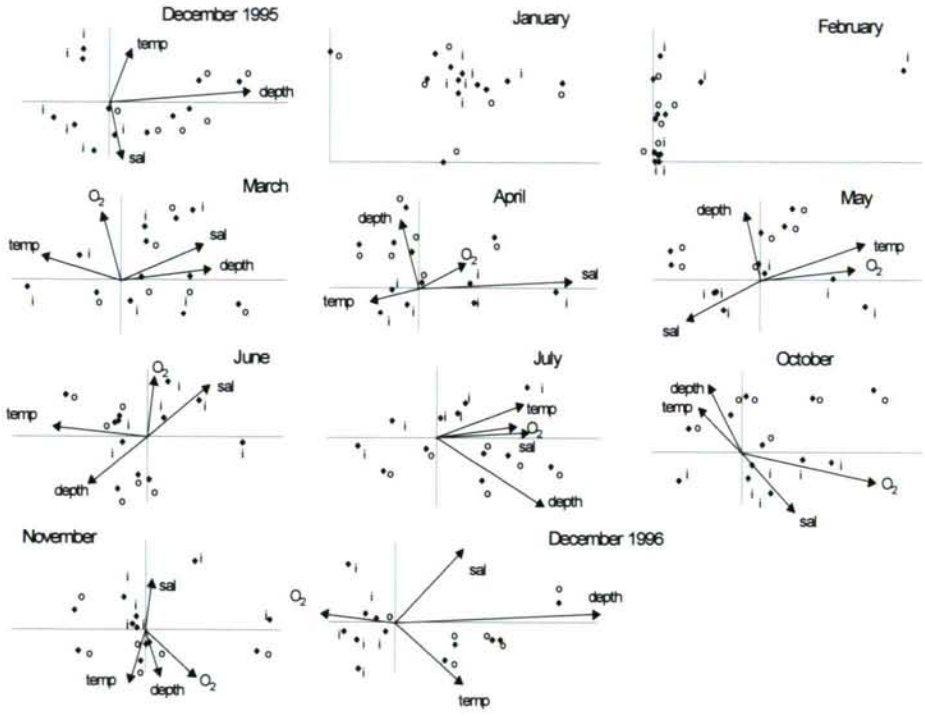

Figure 2. Spatial structure of the fish larvae during December 1995 and March-December 1996 a canonical correspondence analysis was performed and during January and February, through lack of adequate environmental data, and trended correspondence analysis was carried out. (i = inshore sampling stations and o = offshore sampling stations).

We observed a clear spatial structure of the larval fish assemblages; the main gradient of variation was depth, expressed in terms of distance from the coastline (onshore-offshore). This was evident during most of the surveyed period except for the coldest months (January, February, March) (Fig. 2). Low values of correlation were determined between environmental factors, and only during June and October, depth and dissolved oxygen showed a moderate correlation ($0.60 < r < 0.69$). In all cases of canonical analysis, the environmental variables set found with a Monte Carlo global test ($P < 0.05$) were statistically significant. During January and February the DCA showed no spatial segregation of the sampling stations and the length of the first variation axis was reduced in both cases (January 0.21, February 0.27).

The assemblage structure showed three distinct time-related patterns (Fig. 3). The first one was represented by the January-May 1995 (winter-spring) period, the second one included July, October, and November (summer-autumn), and the third or transitional period was represented by June and both December (1995 and 1996). A distinct species assemblage pattern was found to be related to each one of the two main time periods (Fig. 4). The first group, related to the cold period included *Auxis* sp., *Bentosema panamense*, *Cetengraulis mysticetus*, *Opistonema* sp., *Symphurus elongatus*, *Gobionellus* sp., *Dormitator latifrons*, *Bregmaceros bathymaster*, and representatives of Engraulidae and Sciaenidae. A second group is formed by *Harengula thrissina*, *Eutinnus lineatus*, *Vinciguerria lucetia*, *Syacium*

ovale, and representatives of Eleotridae and Pomacentridae; they featured the warm period. The morphotype Gobidae A occurred in both periods.

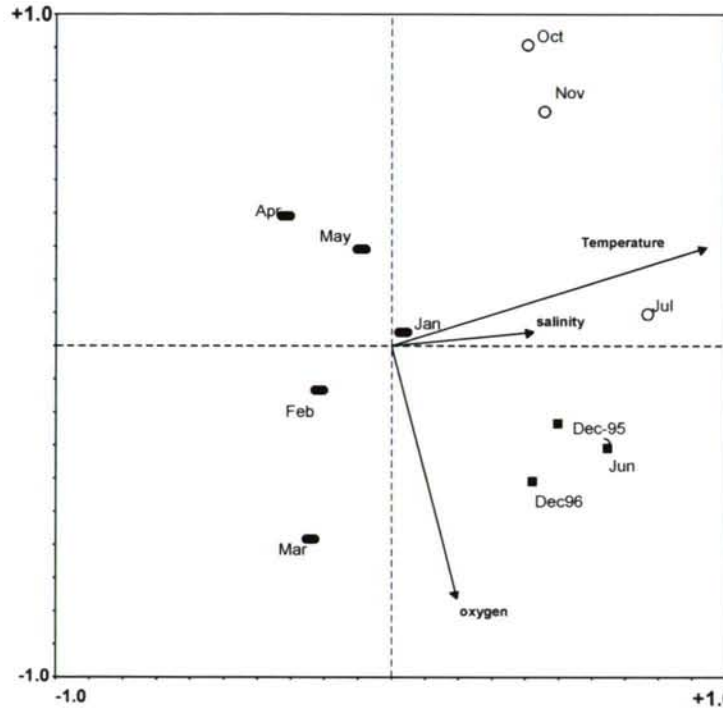

Figure 3. Temporal assemblage patterns in the central Mexican Pacific

A high interset correlation was found between temperature and the first ordination axis (0.79), followed by salinity (0.39). Highest correlation values among environmental variables were shown by temperature and salinity (0.53) and salinity and dissolved oxygen (0.5). A global test based on the Monte Carlo method revealed a

significative relation of the environmental factors used in the ordination analysis ($P < 0.05$). The main axis of environmental variation was represented by the SST thus explaining the seasonal patterns. The response of the ichthyoplankton is considered then to be a result of the dynamic seasonal processes. In all cases, the overall most representative species occurred in both periods, except for *Cetengraulis mysticetus*, with had no records during the summer-autumn period. The ecological affinity of each taxa was defined by its tendency to occur in each of the two main periods (> 50%) (Fig. 6).

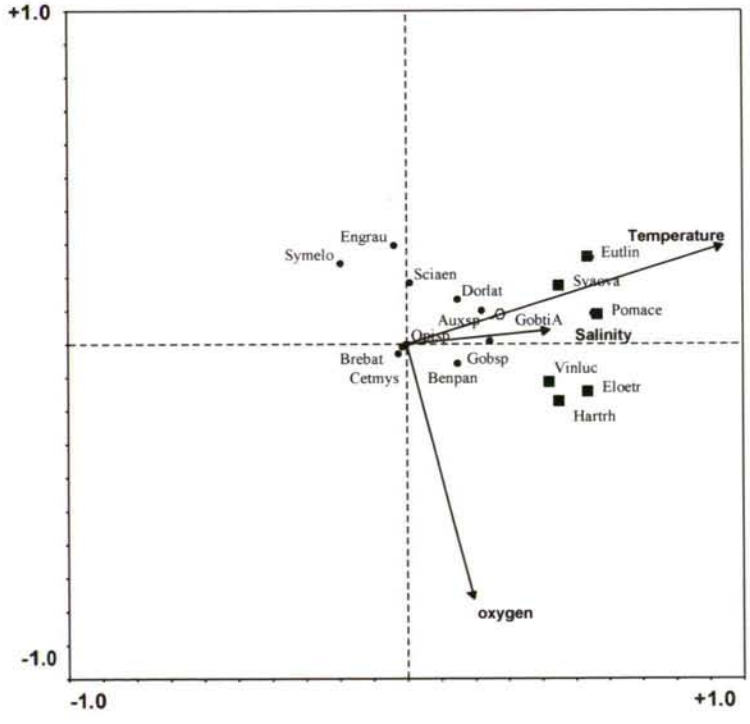

Figure 4. Larval fish assemblages in the central Mexican Pacific. Species abbreviations are defined en Table II.

Up to 92% of the taxa found during this survey is tropical-subtropical, no temperate forms were collected (Table III). Overall, during both periods up to 89 species were recorded and only 39% were shared. During the transitional period 22 species were collected, none of them was particularly abundant, and most are considered to be rare.

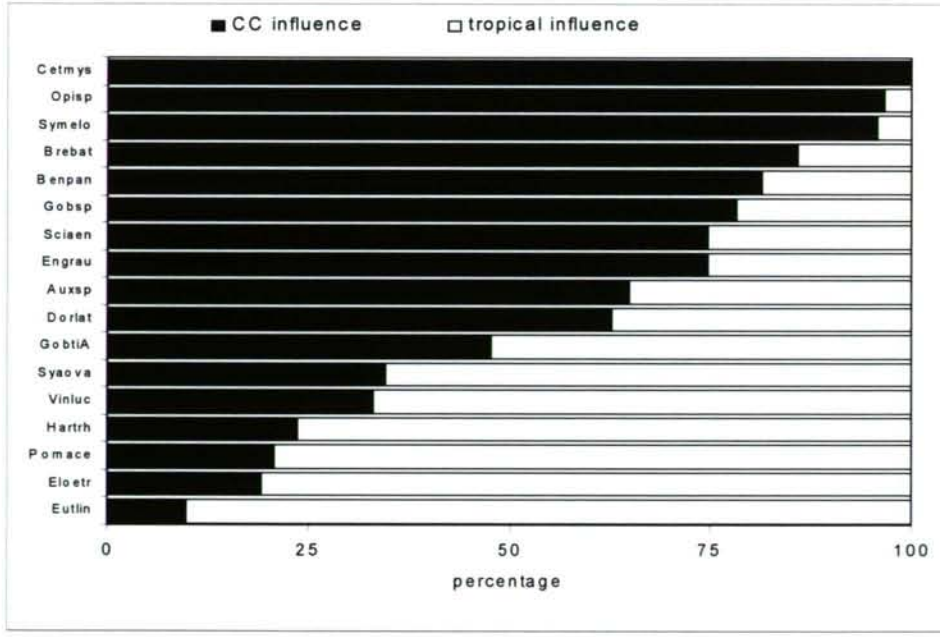

Figure 5. Larval fish affinities in the central Pacific by global period occurrence.

Table III: Biogeographical affinity by period of fish larval assemblage during December 1995 to December 1996 in the central Mexican Pacific; values are % of species.

	Tropical	Subtropical	Tropical-subtropical
CC period	5.9	1.5	92.6
Tropical period	6.2	3.1	90.6
Transition	6.7	4.0	89.2
Total period	5.4	2.7	91.9

38.7% of species were shared among warm and cold periods; 19.8 % of species were found only during transition period.

6.5 Discussion

The spatial pattern of the larval fish assemblages in the surveyed area seemed to be related to coastal dynamic events mainly represented by advective processes. A differential distribution along the inshore-offshore gradient was observed for ichthyoplankton associations during the tropical oceanographic conditions, with a vertical thermic stratification. Conversely, during the colder period, influenced by coastal advective processes, fish larvae assemblages were spatially homogeneous. The time-space distributional patterns of the fish larvae associations found in this survey could be determined by the relation between passive tracers of water mass movement and the behavioral response of the fish larvae, as suggested by Smith and Suthers (1999). An inshore-offshore gradient of fish larval associations has been reported for the CC region

(McGowen, 1993) and for other tropical and subtropical areas of the world (Leis, 1982; Kingsford and Choat, 1989; Smith et al., 1999; Gray and Miskiewicz, 2000).

Larval segregation patterns are generally determined by the reproductive adult migrational patterns, larval drift, and ontogenetic migration (Grioche et al. 1999, Gray and Miskiewicz, 2000). Other particular aspects affecting the composition of the coastal ichthyoplankton communities are: the closeness of reef areas (Kingsford and Choat 1989, Tricklebank et al. 1992, Tilney and Buxton,1994), the presence of estuarine/riverine outflows (Beckley 1986, Tzeng and Wang 1993), the occurrence of oceanographic fronts (Sabates 1990, Sabates and Olivar 1996), and the type of pelagic eggs (Leis and Miller, 1976; Sabates 1990, Suthers and Frank, 1991). In the tropical Pacific, the presence of diverse shallow water habitats such as coastal lagoons, estuaries, relative closed bays, and a well developed rocky shore, and even reef structures, could be a factor emphasizing the across-shelf gradients of ichthyoplankton.

Diel migration has been observed amongst larvae of many taxa of fishes in different marine and estuarine environments (Neilson and Perry 1990), and under both stratified and well-mixed hydrographic conditions (Lyczkowski-Shultz and Steen, 1991). Ontogenetic differences in vertical distribution and migration patterns have frequently been observed (Brewer and Kleppel, 1986; Heath et al.,

1988, Tzeng and Wang, 1993). Our exclusively nighttime sampling effort was designed based on the commonest migrational pattern, with daytime concentrations at lower depths and subsequent surfaceward movements at night; however, the reverse tendency has also been observed in different forms (Lyczkowski-Shultz and Steen, 1991). Hence, ontogenetic behavior factors, independently from hydrographic conditions, could determine, at least partly, the structure of the local fish larvae assemblages and their distributional patterns.

The occurrence of oceanic/slope spawning species such as myctophids, *Vinciguerria* and others, are good indicators of oceanic waters (John, 1984; Belyanina, 1986; Cowen et al., 1993; Chiu and Hsyu 1994, Olivar and Berkey 1994). Myctophids were not particularly abundant, but *V. lucetia* was the seventh most abundant species and occurred in up to 43% of the samples. In the surveyed area, shoreward intrusions and cross-shelf flow are probably transporting most mesopelagic larvae spawned offshore onto the continental shelf, as found by Grioche et al. (1999) in European coastal areas. The reproductive cycles of many mesopelagic fishes are weakly seasonal or non-seasonal (Gjosaeter and Kawaguchi, 1980, Olivar and Beckley,1994), thus offshore mesopelagic ichthyoplankton assemblages tend to show low seasonal fluctuations (Ahlstrom, 1972; Loeb, 1979; Doyle et al., 1993). The year-round dominance of *B. bathymaster* (abundance rank 1) and of *B. panamense* (abundance rank 9) in the surveyed area seems to be a good example of this pattern. Despite the fact that dominant currents

over the shelf flow parallel to the coastline, there is a significative transverse component drifting inshorewards. It varies at different depths, from site to site, and within short time ranges (Huyer et al. 1988, Middleton et al. 1996, Gray and Miskiewicz 2000).

During the July-November period, with the northward flow of equatorial waters, an increased tropical affinity was expected in the area, this effect was reported for copepods (Suárez-Morales et al., 2000). Conversely, the presence of the CC (January-May) would favour the occurrence of temperate or subtropical forms. However, during both periods (CC and tropical), and even during the transitional one, the species composition and biogeographic affinity was stable (see Table 2).

All the species collected during this survey have been previously recorded in either of the three coastal zoogeographic provinces of the Eastern Pacific: Oregonian, Sandieguine, and Panamic (Ahlstrom, 1971; 1972; Moser, 1996). As found in this work, most species of fish larvae in the Gulf of California (Moser et al. ,1974, Avalos-García, 2000) are subtropical-tropical forms. Walker (1960) recognized more than 75% of tropical and subtropical fish species in the Gulf of California (GC). Based on the relatively high endemism of the demersal fauna of the GC, Briggs (1974) separated the Cortes Province. This vision would locate our surveyed area as a transitional zone between the Cortes and the Panamic provinces, in which due to the "border effect", highly speciose assemblages could be expected

due to the mixture of both faunas. However, the observed seasonal recomposition of ichthyoplankton seemed to be more related to the hydrologic patterns, thus explaining why we didn't find a shift of the biogeographic affinity of the species in contrasting conditions. Biogeographic boundaries could also be explained in terms of ecological affinity, as suggested by Longhurst (1998), who included the GC in his Central American Coastal Province based on shared ecological and oceanographic processes.

6.6 References

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Capítulo 7

Plankton and larval fish dynamic prior and during El Niño period (1997-98) in the central Pacific coast of Mexico.

Franco-Gordo, C. Godínez-Domínguez, E. Filonov, A.E. Tereshchenko, I.E. & Freire, J. Manuscrito en revisión. *Progress in Oceanography*.

Plankton and larval fish dynamics prior and during El Niño period (1997-98) in the central Pacific coast of Mexico

Abstract

The temporal and spatial distribution of zooplankton biomass and larval fish recorded during 27 months (December 1995 to December 1998) off the Pacific coast of central Mexico is analyzed. A total of 316 samples were obtained by surface (40-68 m) oblique hauls at 12 sampling sites using a Bongo net. Two well-defined periods are observed; first, a pre-ENSO period (December 1995 to the second half of 1997), and second, the ENSO event, defined by an impoverishment of the pelagic habitat. The highest biomass concentrations occurred at coastal stations only during the normal period. During El Niño period no spatial patterns were found in coastal waters. The months with highest biomass were those in which the lowest sea surface temperature (SST) occurred (January-May) and this pattern was also observed during the anomalous period. A normal seasonal, although attenuated, environmental pattern that enhance phytoplankton (diatoms and dinoflagellates) was prevalent during El Niño event in nearshore waters. During El Niño period the phytoplankton was mainly formed by small diatoms (microphytoplankton) and dinoflagellates were practically absent. The most parsimonious generalized linear models explaining spatial and temporal distribution of larval fish species included the ENSO index (MEI), upwelling index (UI) and shore distance. The environmental

variability defined in a interannual scale by the ENSO events and the seasonal hydroclimatic patterns (defined by the UI) control the ecosystem productivity patterns. The small-scale distribution patterns (defined by a cross-shore gradient) of plankton are related to the hydroclimatic seasonality and modulated by interannual anomalies.

Key words: Mexican central Pacific; inshore phytoplankton, zooplankton, larval fish assemblages; El Niño.

7.1 Introduction

The ENSO phenomenon is an irregular fluctuation that involves the entire tropical Pacific Ocean and global atmosphere (Philander, 1999). ENSO itself consist of an unstable interaction between sea surface temperature (SST) and atmospheric pressure. It results in variations in winds, rainfall, thermocline depth, circulation, and ultimately in biological productivity, modifying feeding and reproduction of fish, birds and mammals (Fiedler, 2002). The 1997-1998 El Niño was, by some measures, the strongest of the 20th century (McPhaden, 1999; Kerr, 1998) and its consequences are still being surveyed.

The knowledge about the El Niño and La Niña events has increased recently and the environmental variability in the Pacific Ocean begins to be well understood (see Philander, 1998; Chavez et al. 1999; 2002; Fedorov & Philander, 2000; Bograd & Lynn, 2001; Lehodey, 2001; Fiedler, 2002) at global and regional scales, while the

knowledge about ecological impacts in the marine habitats remain partial and spatially fragmented. The magnitude, and even the sign, of the response differed among regions. The strongest and the most rapid effects appeared at lower trophic levels, although responses could be observed at several levels (Mullin 1995, Fulton & LeBrasseur 1985, Brodeur et al. 1992). The physical-biological coupling has been reported as main early effect of El Niño, represented by a decrease of nutrient availability (Bograd & Lynn, 2001; Fielder, 1984), and a subsequent decrease of secondary production (McGowan, 1985; Chavez et al. 2002). However, variations from this model of response are found in the North American Pacific coast (Fiedler, 2002); zooplankton biomass increased in the central subarctic Pacific (Brodeur & Ware, 1992; Brodeur et al. 1996) but decreased off Southern California (Roemmich & McGowan, 1995) and did not change substantially off Baja California (Lavaniegos et al. 1998).

Changes in zooplankton biomass are often secondary to changes in species composition. These large and widespread changes affect planktonic communities at multiple trophic levels (Chelton et al. 1982; Graybill & Hodder, 1985; Miller et al. 1985; Mysak, 1986; Pearcy & Schoener 1987; Brodeur et al. 1992; Ainley et al. 1995). Because most of the animals that inhabit marine communities have a planktonic larval phase, one might expect these changes in planktonic communities to affect recruitment rates to populations. However, the evidence for such effects is mixed. In some cases,

recruitment is higher than normal during the El Niño period (Paine, 1986; Roughgarden et al. 1988; Ebert et al. 1994, Connolly & Roughgarden, 1999), but in other cases, recruitment is below levels seen in prior or subsequent years (Tegner & Dayton, 1987; Ebert et al. 1994; Shkedy & Roughgarden, 1997).

During El Niño local upwelling-favorable winds in the eastern tropical Pacific are maintained and even intensified (Enfield, 1981), although the coastal upwelling transports low-nutrient waters due to a deepening of the nutricline remotely forced by Kelvin waves (Barber & Chavez, 1983). Some signals of normal seasonality are evidenced mainly in nearshore waters during El Niño events (Chavez et al. 2002), and their implications in the recover of the previous ecological state have not been well understood. In the North American Pacific, during El Niño events the nutrient levels and productivity of coastal waters suffer a dramatic reduction, the oceanic ecosystem impinges on the shore (Chavez et al. 2002), and the local communities are dominated by tropical or southern species (Lavaniegos et al. 2002; Mackas & Galbraigth, 2002; Marinovic et al. 2002). However the narrow nearshore fringe conserves a relative high productivity (Barber & Chavez, 1983; Chavez et al. 2002; Kudela & Chavez, 2000) and the coastal processes could be determinant for recruitment to local populations (Connolly & Roughgarden, 1999; Marinovic et al. 2002).

The predominant surface current patterns in the central Mexican Pacific are described by Wyrtki (1965), and determine the

hydroclimatic seasonality consisting of the two main phases: the first one is influenced by the California Current, and it is characterized by a cold water mass from January to May; the second phase is a period (July to November) influenced by the North Equatorial Countercurrent and characterized by a tropical water mass (Badan, 1997; Filonov et al. 2000) A third phase is determined by a transition between both previous phases neither one dominating. The coastal ecosystem dynamic response to these seasonal patterns has been studied with respect to zooplanktic biomass and larval fish abundance (Franco-Gordo et al. 2001a; 2001b), larval fish diversity and assemblages (Franco-Gordo et al. 2002; 2003), macroinvertebrate assemblages and diversity (Godínez-Domínguez & Freire 2003; Godínez-Domínguez et al. in press; Godínez-Domínguez et al. in review), coastal fish assemblages (Godínez-Domínguez et al. 2000), and coastal water mass dynamics (Filonov et al. 2000).

Although the El Niño is a global scale process with particularly dramatic oceanographic effects in the tropical Pacific (Chavez et al. 2002), most of the surveys in the North American Pacific coast that approached oceanographic and ecological effects are located in temperate or subartic latitudes (30°-50° N). With exception of some papers in equatorial zones, the effects of ENSO events in the tropical Pacific coasts remain unknown. The present paper describes the oceanographic variability during the 1997-1998 El Niño event in the Mexican tropical coastal waters, and the environmental-biological coupling. Our result will show the prevalence of the normal

intraannual seasonality of the production processes during El Niño event in the nearshore waters. Finally, models to determine the key factors affecting the distribution and abundance of the larval fish assemblage in coastal waters prior and during the ENSO event will be developed.

7.2 Material and methods

7.2.1 Study area

The surveyed area comprises a fringe along the continental shelf off the coasts of Jalisco and Colima, central portion of the Mexican Pacific located between Punta Farallón, in Jalisco (19°19'77"N, 105°00'28"W), and Cuyutlán, Colima (18°58'24"N, 104°13'51"W).

7.2.2 Physical oceanography

The surveys covered a polygonal area (Fig. 1a) on board the research vassel BIP-V equipped with an undulating CTD (SBE-19), that was used continuously for nearly 16-18 hours at an average speed of 6 knots, following the approach of Filonov et al. (1996). Internal waves are known to cause significant vertical variations in all the hydrographic parameters over the continental shelf, so TS characteristics were measured over a finely resolved grid during different phases of the internal waves, and then averaged to minimize their influence (Filonov et al. 2000). Previous measurements in the area had shown that seasonal cycles occur only in the upper 120 m layer (Filonov et al. 1998), whereby surveys were made to 150 m

depth. Each survey consisted of 10 sections 1.5 km apart and perpendicular to the coastline. A typical survey covered 50x15 km (Fig. 1a), yielding about 100 vertical profiles of temperature and salinity. In January 1998, the survey was changed to a cross-shaped (80x30 km track). Normally, the surveys were done on the 15th of each month. A total of 29 surveys were conducted between January 1996 and June 1998, yielding 2374 temperature and salinity profiles (Filonov & Tereshchenko, 2000).

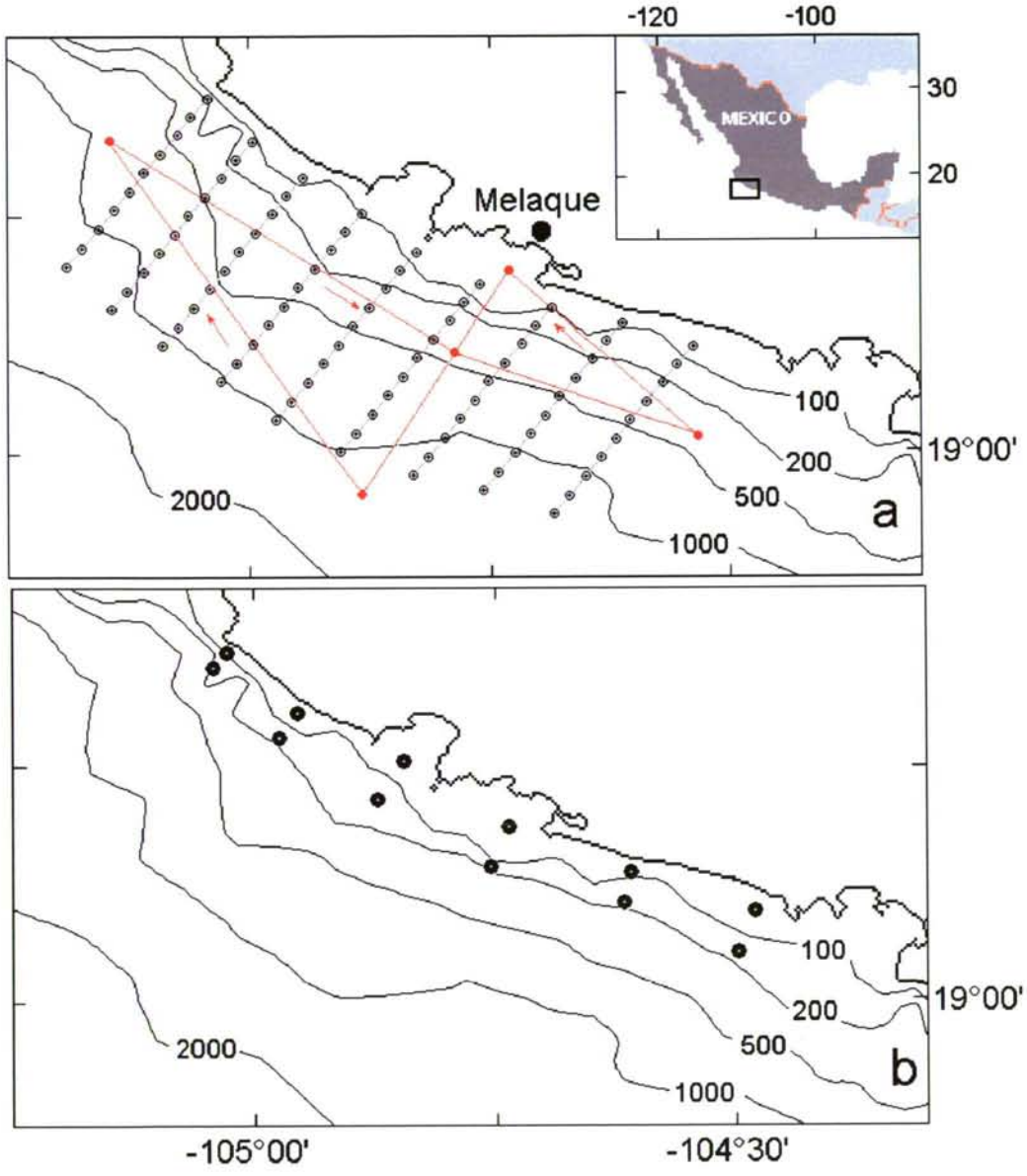


Figure 1. Study area. A) The cruise track corresponding to 1996-1997 is represented by the black dots, and the polygon represented by the red line with arrows was carried out in the 1998 surveys. B) Red dots represent the sites were plankton samples and CTD profiles were taken (December 1995 to Decemeber 1998).

The temperature and salinity variations caused by El Niño event were compared against the monthly sea surface temperature (SST) anomalies in the equatorial part of the Pacific, region B (4°N-4°S, 90°W-150°W) (Monthly Ocean Rep., 1998). For this purpose, vertical integrals for T and S, from 0 to 150 m depth, were taken for each month from January 1996 to June 1998, and the active layer of heat storage per unit surface area was calculated following Mamayev (1975).

7.2.3 Zooplankton cruises

The area was surveyed using a 12-station plan on board the BIP-V oceanographic vessel (Fig 1b) exclusively over the continental shelf. Zooplankton samplings were carried out monthly at night (20:00 to 07:00) from December 1995 through December 1998. No samplings were made in some months due to adverse climatological conditions. Zooplankton tows were performed following Smith & Richardson (1977). Samples were collected by means of a Bongo net with a 0.505 mm mesh size hauled obliquely from a depth of 42-86 m, which implied a sampling range of 60-90% of the water column in the surveyed area. A digital flowmeter was adapted to the net mouth in order to estimate the volume of water filtered. Previously to each tow, a profile of temperature and salinity was recorded using a CTD profiler SBE-19. Samples were fixed and preserved in a 4% formalin solution buffered with sodium borate (Griffiths et al. 1976). Samples

collected were immediately processed to obtain the zooplankton biomass in order to avoid volume changes associated with long-term preservation. Samples were processed according to the displacement volume method (Beers, 1976). Organisms measuring over 3 cm length were excluded from the samples; gelatinous zooplankters below this size were included in the biomass estimations. Estimated biomass values are reported as cm^3 per 1000 m^3 of filtered water. Fish larvae were sorted and abundance data were standardized into number of larvae per 10 m^2 (Smith & Richardson, 1977). Two-way ANOVAs were carried out to determine differences in larval fish abundance and zooplanktic biomass along months of the year and coastal distance (inshore vs offshore). Separate analyses were carried out for the previous and El Niño period.

7.2.4 Phytoplankton sampling

During 1998, samples of water at 0 and 25 m depth were taken previously to zooplankton tows, using Niskin bottles. Diatom and dinoflagellate abundance were quantified following the Utermöhl procedure (Hasle, 1978). Two-way ANOVA tests was employed to determine the effect on cell abundances of diatoms and dinoflagellates of time (sampling months) and coastal distance (inshore vs offshore).

7.2.5 Modeling the spatial and temporal variability of the larval fish assemblages

7.2.5.1 Selection of environmental variables

The following environmental variables were used:

-Inshore and offshore sea surface temperature (SST) and salinity.

-The Multivariate ENSO Index MEI (Wolter & Timlin, 1993; 1998) as an indicator of El Niño/La Niña conditions in the tropical Pacific. The MEI is based on six highly correlated observed variables in the tropical Pacific: SST, atmospheric sea level, pressure (SLP), surface winds, zonal and meridional surface air temperature and total cloudiness. (Details on the computation of the MEI are available at: www.cdc.noaa.gov/~kew/MEI/mei.htlm).

-The upwelling index UI (at 21° N, available in www.pfeg.noaa.gov).

We consider that these variables integer simple and complex, short and long term, local and wide scale environmental variability, and could define an adequate environmental framework for local ecological processes. A Principal Component Analysis (PCA) was employed to determine the similarity among variables, to reduce their number for posterior GLM analyses and to reduce the dimensionality of resultant models. Because UI and MEI are estimated for different geographical areas (MEI is a complex index based on equatorial indicators, while UI is defined by environmental variability 1° to the

north from the study area), a crosscorrelation analysis of MEI, UI and local environmental variables was performed to determine the possible lag of the signals of MEI and UI in relation to local environmental variability.

7.2.5.2 Models to explain variability in abundance of fish larvae

Generalized Linear Models (GLM) were used to analyze the spatial and temporal patterns of the variability of the abundance of fish larvae. The following independent variables were included: environmental variables (selection criteria are explained previously), a linear temporal trend (number of months from December 1995), coast distance (inshore vs offshore), and local hydroclimatic seasonality (tropical, transition and subtropical-temperate seasons). These variables define the most significant components of spatial, intrannual and interannual variability in the coastal ecosystem. Model selection was based in the best subset procedure using the Akaike information criterion (AIC), and a normal log link was assumed.

7.3 Results

7.3.1 Vertical temperature and salinity profiles

The main change in the vertical distribution of temperature and salinity occurred from June to December 1997 (Fig. 2). During July-August 1997, the lowering of the thermocline was distinctly smoother, and the increase in salinity, from 34 psu (practical salinity units) at the surface to 34.7 psu at 150 m depth, was almost linear. In September

1997, the vertical temperature profile became noticeably concave downward, which suggests the formation of a homogenous layer of Pacific Tropical Surface Water (PTSW), which grew steadily throughout the entire fall, reaching a thickness of 70 m by December 1997 reaching a temperature of 28.5°C. At the same time, salinity fell to 33.5 psu at the surface, while in the homogeneous layer it increased to 34 psu.

The strongest impact of El Niño occurred in January 1998, and the PTSW filled the entire upper 80 m layer with a temperature of 27.5°C and a salinity <34 psu. For comparison, in January 1996, the surface temperature was 25.5°C and the top of the thermocline was at a depth of 25 m. Even at 90 m, temperature was 15°C and salinity 35 psu (Fig. 3).

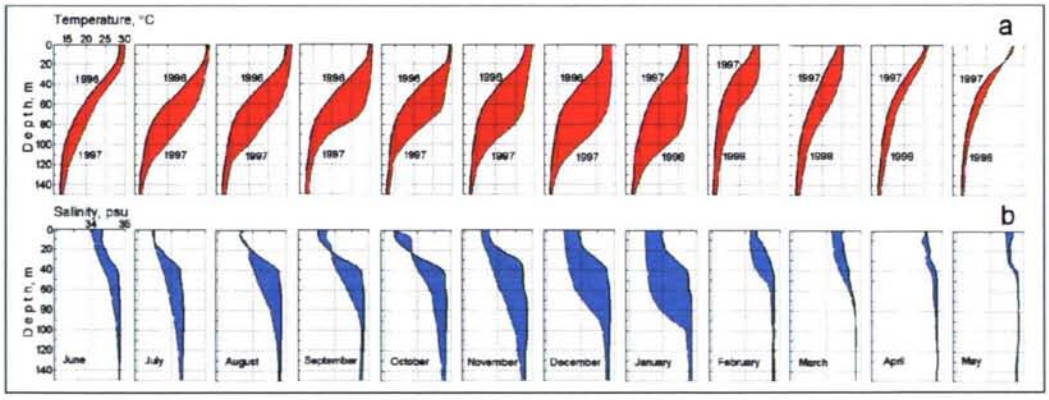


Figure 2. Mean (a) temperature and (b) salinity profiles based on monthly surveys for the period June 1996 to June 1998.

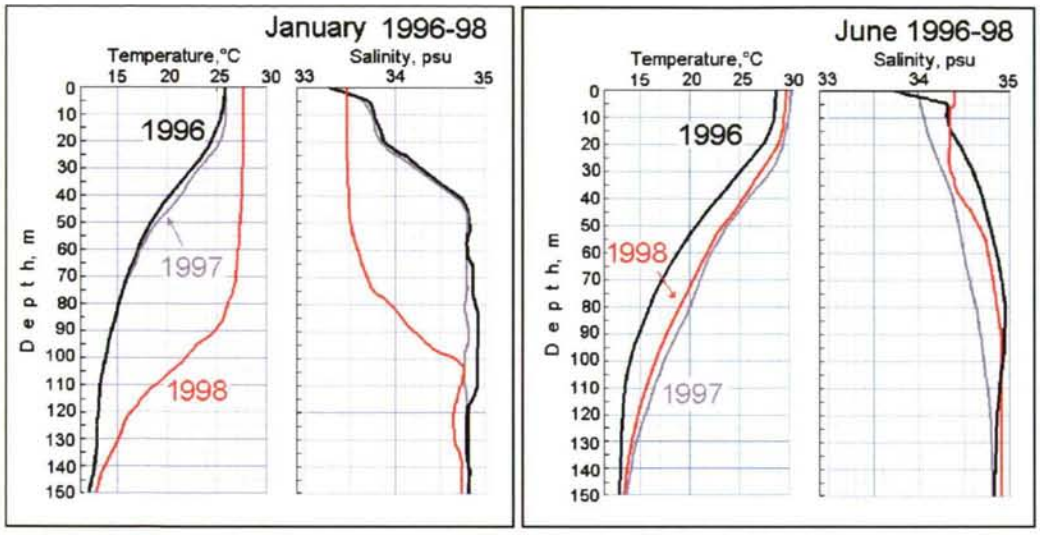


Figure 3. Mean temperature and salinity profiles that illustrate the interannual variability (January and June 1996, 97 and 98) produced by the El Niño event 1997-1998 off central Mexican Pacific waters.

7.3.2 The evolution of El Niño event and heat storage

During the 1997-1998 El Niño event, the rate of change of heat storage, the rise in temperature and the drop in salinity within the upper layer agree well with SST anomalies time series in the Pacific region B. In January 1998, the temperature was 7.6°C higher and salinity was 0.5 psu lower than in January 1996. Over the same period, the head storage of the oceanic active layer had increased from 10.1 to 15.3 CJ/m^2. During the entire year of 1996, the SST anomalies in region B were close to zero (Fig. 4). Beginning in 1997, their values became positive and continued to increase until December, when they peaked at +4.5°C. Starting in January 1998, they decreased rapidly and attained almost zero in June. El Niño had

the strongest impact on the Mexican coast within a month after the El Niño Index reached its peak in region B.

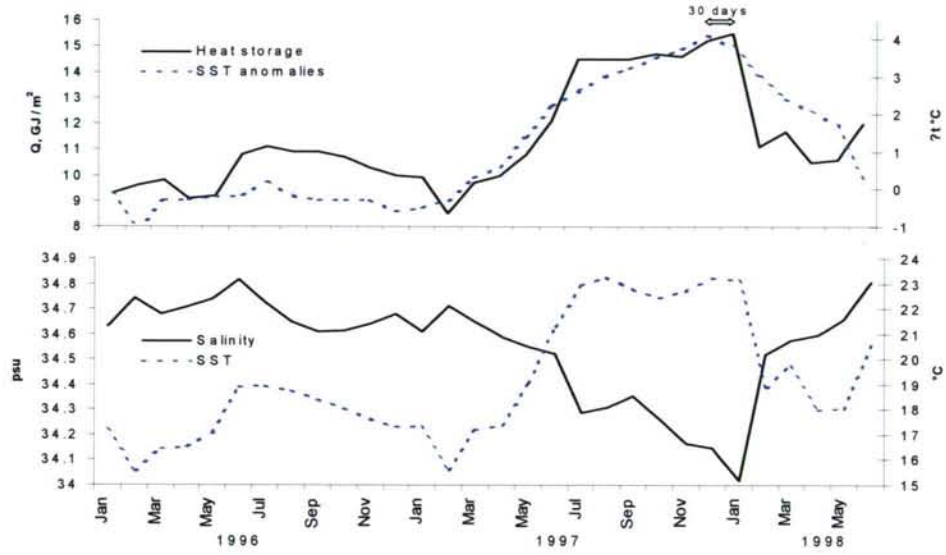


Figure 4. Monthly values of temperature, salinity and heat storage Q variations in the 0-150 m and SST anomalies in the equatorial region B (4°N-4°S; 90°W-150°W), period 1996-1998.

7.3.3 Environmental-biological coupling. Relation between environmental variability and zooplankton biomass and larval fish abundance

Two well-defined periods were observed in the monthly zooplanktic biomass and larval fish abundance time series; first, a pre-ENSO period (December 1995 to the spring of 1997), and second, the ENSO event, defined by an impoverishment of the pelagic habitat that started suddenly in the summer of 1997 (Fig 5). During the pre-El Niño period, despite of the significant differences in larval fish abundance and zooplanktic biomass among months ($p<0.05$; Table 1), the highest abundance and biomass concentrations occurred at inshore stations. During El Niño period, monthly differences were observed in both abundance and biomass, but no significant difference was found between offshore and inshore stations. The months with the highest biomass were those in which the lowest SST occurred (January-May) and this pattern still persisted during the anomalous period. This was the same period in which the California Current was strongest and advective processes were active along the outer shelf favouring upwelling of colder, relatively nutrient-richer, waters that promoted an overall local increase of zooplankton activity and abundance. The moderate peaks of larval fish abundance and zooplanktic biomass observed from January to May during the El Niño period suggest the prevalence of environmental conditions that enhance in normal periods the primary and secondary production in coastal waters.

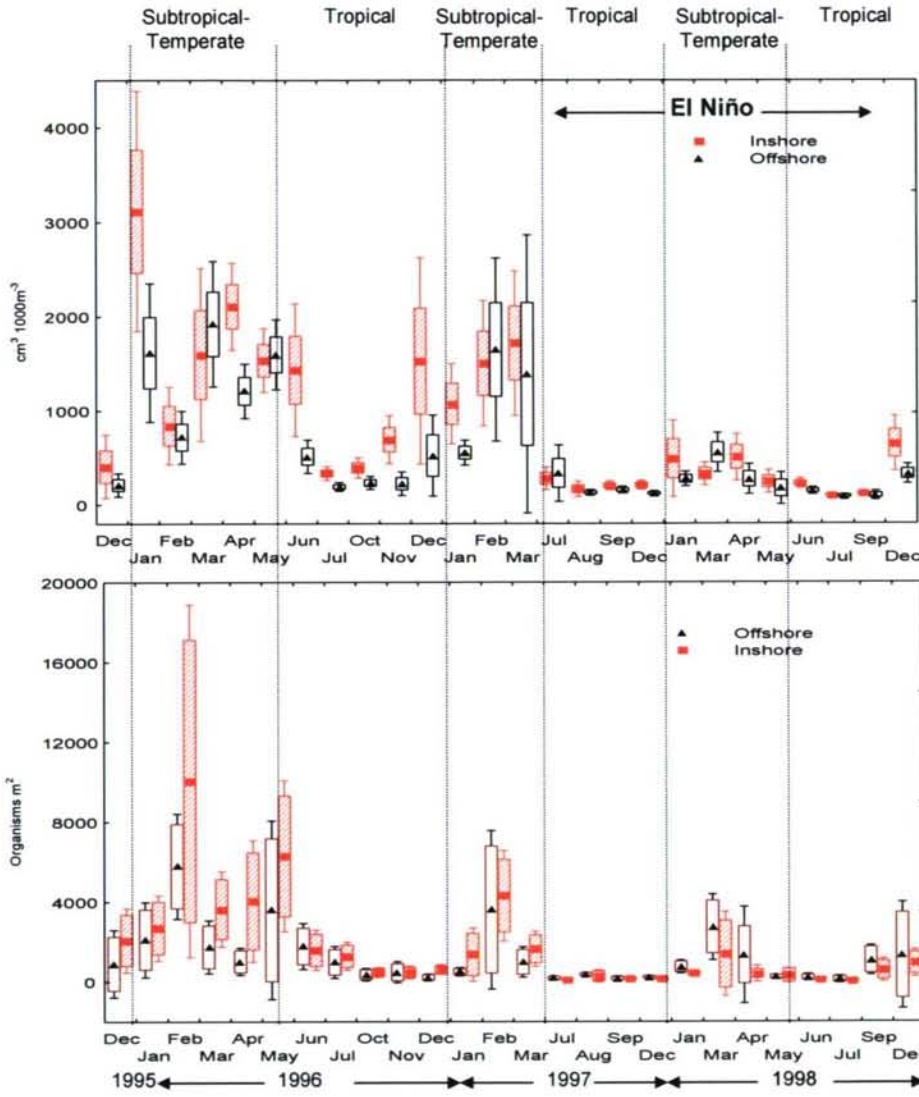


Figure 5. Monthly variability of the zooplanktic biomass and larval fish abundance during and prior the El Niño 1997-98 event. Mean offshore and inshore values are represented by empty boxes and dashed boxes respectively. Vertical lines represent the 95% confidence interval and boxes one standard error.

Table 1. Results of ANOVAs comparing larval fish abundance and zooplankton biomass among sampling months and distance to shore during El Niño 1997-98 and pre El Niño periods

	Larval fish abundance						Zooplankton biomass					
	El Niño period			pre El Niño period			El Niño period			pre El Niño period		
	df	F	p	df	F	p	df	F	p	df	F	p
Intercept	1	38.42	< 0.001	1	143.64	< 0.001	1	174.72	< 0.001	1	337.44	< 0.001
Month	11	3.63	< 0.001	13	8.51	< 0.001	11	4.50	< 0.001	13	8.49	< 0.001
Distance	1	3.29	0.072	1	9.23	0.003	1	3.16	0.078	1	11.59	< 0.001
Month*distance	11	0.54	0.875	13	0.84	0.622	11	1.28	0.242	13	1.29	0.225
Error	124			140			124			140		

Table 2. Results of ANOVAs comparing phytoplankton abundances among sampling months and distance to shore during 1998.

	Sea surface						25 m depth					
	Diatom			Dinoflagellate			Diatom			Dinoflagellate		
	df	F	p	df	F	p	df	F	p	df	F	p
Intercept	1	30.274	< 0.001	1	42.076	< 0.001	1	111.65	< 0.001	1	39.34	< 0.001
Distance	1	1.034	0.312	1	0.132	0.717	1	4.42	0.039	1	0.04	0.837
Month	8	6.187	< 0.001	8	4.405	< 0.001	7	14.47	< 0.001	7	4.75	< 0.001
distance*month	8	0.256	0.978	8	0.490	0.860	7	2.05	0.060	7	0.92	0.498
Error	84			84			74			74		

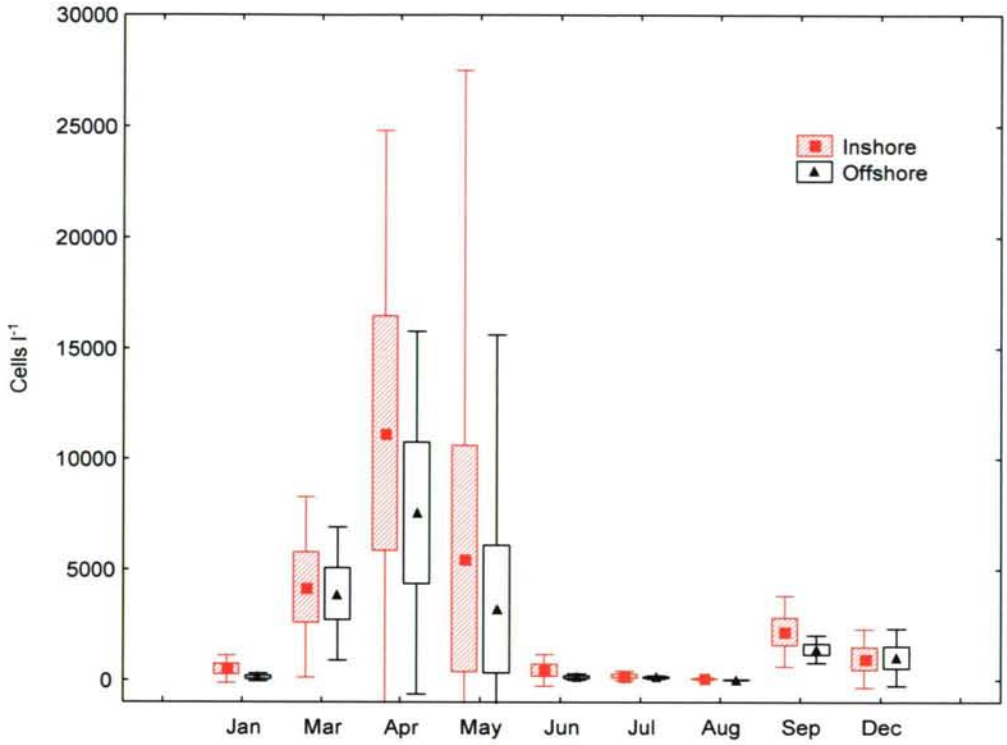


Figure 6. Monthly mean values of phytoplankton represented by the sum of dinoflagellates and diatoms in the inshore and offshore sites. Boxes represent one standard error and vertical lines the 95% confidence interval.

7.3.4 Seasonal primary production pattern during El Niño event

Diatoms were several times more abundant than dinoflagellates at both depths (0 and 25 m). There were no differences in abundance between inshore and offshore diatoms and dinoflagellates, however the differences along time were significant ($p<0.05$; Table 2). The highest diatom abundance was found from March to May (Figure 6). No clear patterns were observed in the case of dinoflagellates due their lower abundance.

7.3.5 Models of the variability of zooplankton biomass and larval fish abundance

7.3.5.1 Relation among environmental variables

The PCA (Fig. 7) shows that both inshore and offshore, salinity and SST, presenting a high correlation with the first principal component (PC), have a high predictability among them and could be reduced to one variable. We selected for GLM analyses the inshore SST because temperature is one of the most commonly used oceanographic data and easy to record. MEI and UI are associated mainly with the second PC but they seem to be associated to different oceanographic processes. The cross-correlation analysis indicates that the highest correlation between SST and UI was obtained with a lag of -1 month, meaning that climatic changes that control the upwelling processes occur one month before at one degree of latitude in the north (Fig. 8). A clear six-month harmonic component in the variables was observed. The highest correlation value between SST and MEI was with a positive lag of MEI, which indicates that the ENSO signal takes one month to arrive to the study area, and no harmonic components were observed. SST and salinity showed their highest cross-correlation with a lag of -1 month.

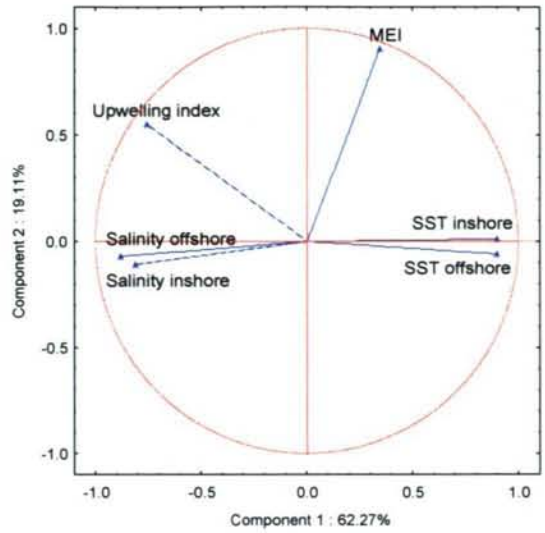


Figure 7. Principal component analysis of the environmental variables taken simultaneously with the plankton samplings (salinity and SST) and other oceanographic variables representing the El Niño signal (MEI) and the regional Upwelling index (UI).

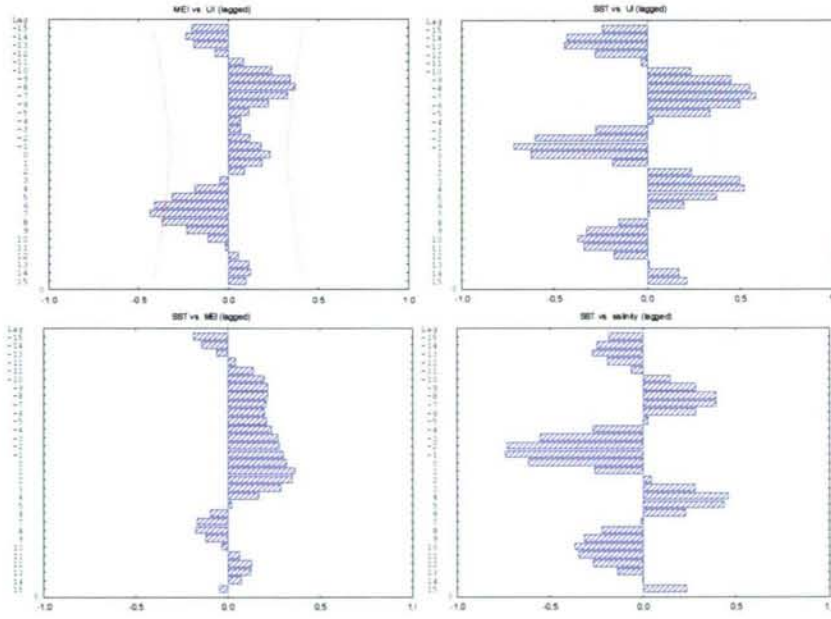


Figure 8. Cross-correlations between the environmental variables employed to model the variability of the planktonic community.

7.3.5.2 Generalized linear models of zooplankton and larval fish abundance

MEI, UI and SST were the most influent variables in plankton and larval fish abundance according to their frequency of appearance in the most parsimonious GLM models (Table 3). Time trend, distance to the coast, season, and the interaction of season and distance constituted a secondary group. Total larval fish abundance, zooplanktic biomass, and the abundances of *Bregmaceros bathymaster*, Engraulidae and Sciaenidae responded negatively to MEI (Table 4). The rest of species were related positively to MEI. The UI was positively related with the taxa that were negatively related with MEI. The SST was negatively related with most of the taxa and only was positively related with *Auxis* sp. *Vinciguerria lucetia*, *Caranx* spp. *Euthynus lineatus*, *Lutjanus* spp., and Pomacentridae. A clear negative trend was showed by *V. lucetia, Benthosema panamense, Gobionellus* sp., *E. lineatus, Harengula thrissina* and *Auxis* sp. Inshore stations were positively related with zooplanktic biomass, larval fish abundance, *B. bathymaster*, *H. thrissina* and *Lutjanus* spp. (see Figure 9). The taxa associated to offshore stations were *B. panamense*, *Syacium ovale*, *V. lucetia*, Engraulidae, *E. lineatus* and Pomacentridae. The variables responding positively to the California Current period were zooplanktic biomass, larval fish abundance, and the abundances of *V. lucetia, B. panamense, E. lineatus*, Pomacentridae, Gobidae and *B. bathymaster*.

Table 3. Generalized linear models (GLM) of abundance of zooplankton biomass and larval fish abundance (total and for each taxa). Variables included in the most parsimonious models selected using best subset procedure based in the Akaike information criterion ($p < 0.01$ in all cases) are showed.

	MEI	UI	SST	shore distance	season	trend	interaction*	df
Larval fish abundance	x	x		x	x			5
Zooplanktic biomass	x	x	x	x	x		x	8
Bregmaceros bathymaster	x	x		x	x			5
Vinciguerria lucetia	x	x	x	x	x	x	x	9
Benthosema panamense	x	x	x	x	x	x		7
Gobionellus sp.	x	x	x		x	x	x	7
Lujanus spp.	x	x	x	x	x	x		7
Syacium ovale	x	x	x	x		x	x	7
Euthynus lineatus	x	x	x	x	x	x		6
Harengula thrissina	x	x	x	x	x	x		6
Auxis sp.	x	x	x			x	x	5
Pomacentridae	x	x	x	x	x			5
Engraulidae	x	x	x	x				3
Sciaenidae	x	x	x					1
Gobidae	x	x			x	x	x	7
Dormitator latifrons			x				x	3

* = Distance*season interaction

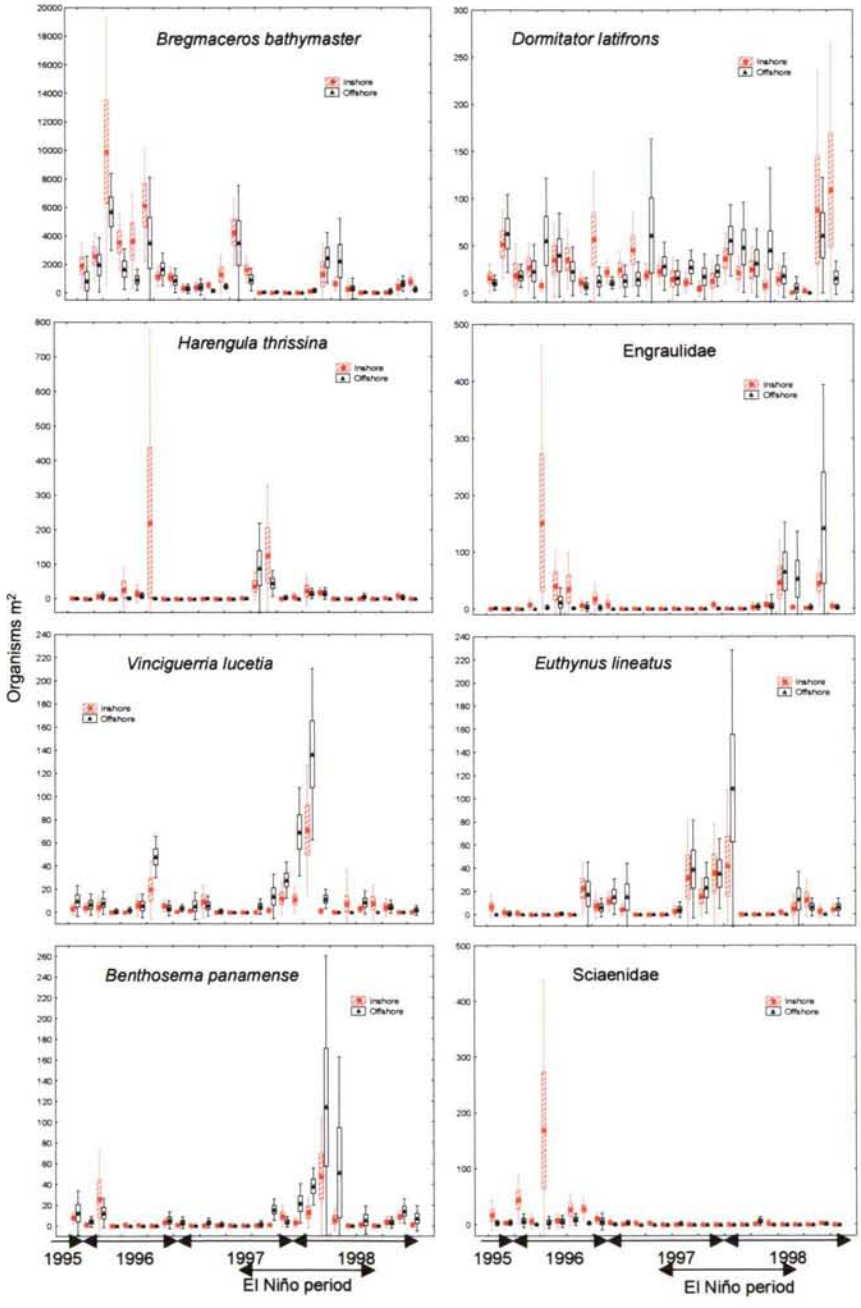
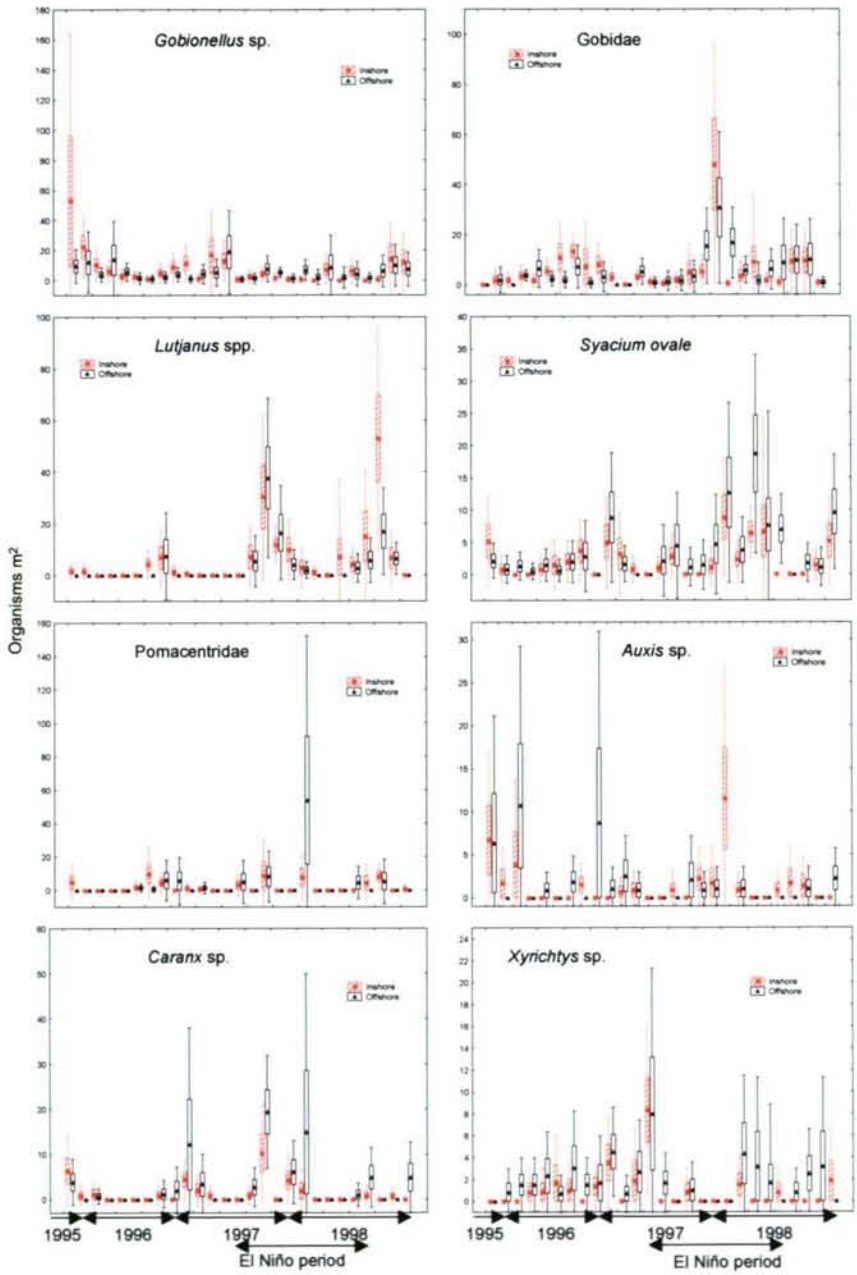


Figure 9. Time series of abundance of the most important larval fish taxa during and prior the El Niño 1997-98 event in both inshore and offshore sites. Boxes represent one standard error while vertical lines represent the 95% confidence interval.



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7.4 Discussion

7.4.1 Oceanographic setting

A distinct change in the hydrological pattern of the area, most probably caused by El Niño, became clear in July 1997. A weakening of the trade winds had resulted in a displacement of the Subsurface Equatorial Water toward the Mexican coast (Filonov et al. 2003). This water mass has relatively high temperature and low salinity, with TS characteristics identical to those of the Pacific Tropical Surface Water (PTSW). Eventually, this water mass drove the local water out of the upper layer.

7.4.2 Temporal variability of the zooplankton biomass and larval fish abundance

A clear declining interannual trend was observed in the zooplanktic biomass and the larval fish abundance (see Figure 5), but a seasonal response was also observed. The length of the series limits the linear trend observed and probably the resilient response of the plankton community to the ENSO events follow a wider temporal period. In the North American Pacific coast the Pacific Decadal Oscillation (PDO) and ENSO events determine the multi-year environmental changes, which produce extraordinary influences in primary and secondary production and fish populations (Smith & Moser, 2003). In the California Current zone (CC), there are several long-term, decadal, plankton series: primary production (Hernández

et al. 2003), tunicates (Lavaniegos & Ohman, 2003), copepods (Peterson & Keister, 2003), eupahusiids (Brinton & Townsend, 2003) and larval fishes (Smith & Moser, 2003), and several temporal components has been identified. Besides those indicators of the pelagic ecosystem as zooplanktic biomass or abundances of different groups are sensitive to the different temporal scales, the main characteristic of the community response could be determined by the differentiated response of the species.

There are three main temporal variability sources in the Northeastern Pacific waters; the decadal scale associated to the regime shift, the interannual scale associated to the ENSO events and the hydroclimatic seasonality. However the degree of influence, at least in the interannual scale, depends of the geographic location: ENSO-scale variability (2 to 7 yr) is dominant in the eastern equatorial Pacific and decadal scale variability (10 to 30 yr) is dominant in the northeastern Pacific (Fiedler, 2002). The studied area is located at the mouth of the Gulf of California and their seasonal hydroclimatic cycle shows an influence of tropical and subtropical water masses (Filonov et al. 2000; Filonov & Tereshchenko, 2000) and the zooplanktic community is related to this variability pattern (Franco-Gordo et al. 2001a; 2001b; 2002; 2003). However there is not information available to determine if decadal or interannual variabilities are the most influent sources, due the lack of long-term time series of oceanographic and biological variables in the central Mexican Pacific.

The impoverishment of the pelagic habitats is one of the most cited effects of the ENSO events (Chavez et al. 1999), and produce a decline of primary, secondary and fish production, producing a ecosystem reorganization (Fiedler, 2002), however the sign and even the magnitude of the change could vary with no geographical pattern. The zooplankton biomass decreased markedly in our case during El Niño, and similar results were recorded in the CC zone (Lavaniegos et al. 2002; Mackas & Galbraith, 2002; Roemmich & McGowan, 1995). However an increase was reported in the central subartic Pacific (Brodeur & Ware, 1992; Brodeur et al. 1996), and no changes were observed off northern Chile (González et al. 2000) and off Baja California (Lavaniegos et al. 1998). The variability of the zooplanktic biomass during ENSO events could be affected by the species composition: in Chile no changes of zooplankton biomass were observed but the relative abundance of small-sized copepods increased (González et al. 2000), and in a region of CC zone higher biomasses were due to high abundance of warm-affinity salps (Lavaniegos et al., 1998) and copepods (Lavaniegos et al. 2003). Changes in zooplankton biomass are often secondary to changes in species composition (Fiedler, 2002). For several zooplankton groups, species shifted their distribution along CC zone during the El Niño events (1958-1959, 1978-1979, 1982-1983, 1986-1987 and 1997-1998), where cold-water California Current species were less common (Table 5). In fact one of the main effects in the planktonic community during El Niño event in subtropical and temperate areas is

the tropicalization of the species composition. Seasonal fluctuations in the zooplanktic biomass and larval fish abundance are widely reported in the Pacific Ocean (Chiba & Saino, 2003; Rodríguez-Graña & Castro, 2003; Franco-Gordo et al. 2001a; 2001b) inclusive during the ENSO events (Mackas & Galbraith, 2002) as our results show.

Table 4. Parameters of generalized linear models fitted to a) zooplankton biomass, larval fish abundance and most abundant larval fish species, and b) target species of the local small-scale fisheries. Significant effects ($p < 0.05$) are showed in red.

a	Level of effect	Zooplanktic biomass	Larval fish abundance	*Auxis sp.*	*Benthosema panamense*	*Bregmaceros bathymaster*	*Dormitator latifrons*	Gobiidae	*Gobionellus sp*	*Harengula thrissina*	*Sycium ovale*	*Vinciguerria lucetia*
Intercept		7.73	6.39	-88.81	66.66	6.19	5.67	4.29	3513.30	158.15	6.43	21.30
MEI		0.46	0.80	4.33	24.36	0.95	0.10	0.41	88.20	23.44	0.49	1.25
UI		0.00	0.01	-0.11	0.02	0.01	0.00	0.01	-5.23	0.10	0.01	0.01
SST		0.06	0.00	3.40	2.19	-0.01	-0.10	-0.30	-127.89	6.41	0.47	0.86
Trend		0.00	0.00	-0.94	3.50	0.02	0.00	0.32	-12.36	-3.59	0.36	0.16
Distance	Inshore	0.28	0.14	0.28	-0.85	0.11	-0.03	-0.17	56.51	1.51	-1.01	0.62
Season	Transition	0.06	-0.02	0.71	8.29	0.03	-0.04	-0.06	46.20	23.51	0.03	0.34
Season	Calif. Current	0.49	0.39	13.60	2.94	0.47	0.23	0.73	7.40	-53.71	0.62	3.45
Distance*season	Inshore*transition	0.18	-0.03	0.49	-0.14	-0.06	0.09	-0.48	57.63	2.37	-0.54	-0.26
Distance*season	Inshore*Calif.Current	-0.23	0.12	-0.85	0.07	0.15	0.24	0.36	-41.43	1.48	0.64	0.32

b	Level of effect	*Caranx spp.*	Engraulidae	*Euthynus lineatus*	*Lujanus spp.*	Pomacentridae	Sciaenidae
Intercept		4.95	-0.32	-68.62	64.62	88.40	51.76
MEI		24.61	-35.19	13.32	2.66	0.77	-67.34
UI		-0.03	0.07	0.05	0.02	-0.02	0.13
SST		0.19	0.27	2.01	1.23	2.78	1.35
Trend		-3.92	-2.41	-0.98	1.09	0.42	-0.50
Shore distance	Inshore	-0.43	-0.08	0.23	1.12	1.56	-0.47
Season	Transition	8.17	-11.40	3.91	-0.99	4.35	4.11
Season	Calif. Current	7.88	-6.37	8.01	-4.11	8.58	-25.81
Distance*season	Inshore*transition	0.50	-2.88	0.12	-0.81	2.29	-0.20
Distance*season	Inshore*Calif.Current	-0.61	1.93	-0.22	1.78	0.66	1.95

7.4.3 The prevalence of an attenuated normal seasonality during El Niño event in inshore waters

The monthly abundance of diatoms and dinoflagellates, zooplankton biomass and larval fish abundance during 1997-98 showed a prevalence of normal, although attenuated, hydroclimatic patterns during El Niño. The prevalence of normal seasonal patterns in the assemblages of coastal fish (Godínez-Domínguez et al. 2000; Madrid & Sánchez, 1997) and soft-bottom macroinvertebrates (Godínez-Domínguez et al. in review), has been reported for the central Mexican Pacific. The decreases in primary production are directly linked to changes in nutrient supply, which evidence a physical forcing driving a biological response and the effects off Central (Chavez et al. 2002) and Southern California (Bogrard & Lynn, 2001) were similar to those in the equatorial Pacific (Chavez et al. 1999). During El Niño period diatoms were more abundant than dinoflagellates and the same occurred in central California, where dinoflagellates and picophytoplankton showed low abundances during El Niño (Chavez et al. 2002). According to these authors the high diatom abundance supports the conclusion that coastal processes (e.g. upwelling) that favor diatoms must have remained active during El Niño in inshore waters, however, the carbon to chlorophyll ratio increased greatly and primary production per unit of carbon decreased dramatically, indicative of nutrient-limited phytoplankton.

7.4.4 Cross-shore distribution of the primary and secondary production and larval fish abundance

A clear inshore-offshore structure of the larval fish and zooplankton community was observed during the pre-ENSO period, and inshore stations showed the largest abundances. During the ENSO period no spatial structure was found. Only for diatoms at 25 m depth, the inshore-offshore differences were significant. During the non-ENSO period, an inshore-offshore seasonal pattern has been also observed elsewhere for the zooplanktic biomass, and the larval fish abundance and assemblages in the study area (Franco-Gordo et al. 2001a; 2001b; 2003). This small-scale spatial pattern seems to be related to coastal dynamic events mainly represented by advective processes (Franco-Gordo et al. 2003), and during the tropical oceanographic conditions, with vertical thermal stratification, a well-differentiated inshore-offshore gradient is observed. The coastal advective processes during the cold season produce a spatial homogenization of the zooplankton biomass and the larval fish assemblage. We hypothesize that the coastal processes that control the cross-shore transport are disarranged. The typical ENSO effects are defined by a strong vertical and horizontal stratification, which modify the advective regime. However in the coastal waters upwelling continues, but the upwelled water has low nutrient concentrations and the productivity declines sharply (Chavez et al. 2002). These factors could explain the prevalence of a normal attenuated seasonality, but with a weak coastal horizontal stratification.

7.4.5 Response of the larval fish species and zooplankton biomass to environmental variability

Broad-scale interannual processes appear to control environmental variability in the studied area, and together with temporal seasonality determine the fluctuations of the larval fish abundance and zooplankton biomass. A small-scale spatial pattern defined by the cross-shore distribution is controlled firstly by hydroclimatic seasonality and it is modulated by interannual anomalies.

The most parsimonious GLM models for larval fish abundance included the environmental variables MEI and UI, the seasonal and spatial (cross-shore) variability. These results reinforce the assumption that the seasonal component determine the fish production patterns, and is affected by interannual processes as El Niño event. Both UI and hydroclimatic seasons define the intraanual cycle that determine the ecosystem productivity patterns. Spawning timing and location, the larval life duration, larval behaviour and coastal processes affect the composition and spatial distribution of the larval fish community (Mullin, 1993), however during El Niño event, the composition and spatial structure of the larval fish community are affected mainly by the physical environmental stress and the changes in transport patterns in North American coasts (Smith & Moser, 2003; Sánchez-Velasco et al. 2000), and Chile (Rodríguez-Graña & Castro, 2003). The zooplankton biomass was sensitive to the SST and cross-shore interaction, which suggests the local influence on the secondary production. This interaction defines

the influence of the coastal processes in the vertical and horizontal stratification and as consequence in the primary and secondary production and the transport. It has been hypothesized that spawning strategies in marine fish populations have evolved in synchrony with prevailing oceanographic conditions to give rise to persistent multi-species assemblages of fish larvae (Parrish et al. 1981; Frank & Leggett, 1983; Doyle et al. 1993), and for this reason the larval fish species change in a similar way in relation to primary and secondary production patterns, spatial and seasonal, but are strongly affected by interannual global processes.

An increasing time trend was included in the models of *Lutjanus* spp., *S. ovale* and Gobidae. The *Lutjanus* species are the most valuable target species of the small-scale fisheries in the region, and their catches fluctuate strongly with important peaks inclusive during La Niña 1999 event (Rojo-Vázquez et al. in review). The linear trend of the lutjanid larvae could not be easily related with the abundance of the reproductive stock mainly due to catchability changes of the coastal fishes (demersal and pelagic) during ENSO events (Godínez-Domínguez et al. 2000; Rojo-Vázquez et al. in review). Interannual recomposition or geographic shifts in larval fish species in the CC zone have been reported by Smith & Moser, (2003). *V. lucetia* is one of the dominant mesopelagic species in the entire Eastern Tropical Pacific and became one of the most abundant larval taxa in the Southern California Bight during the two last decades (Smith & Moser, 2003). According to these authors, the recomposition of the

larval fish assemblages along the interannual and longer periods, where a regime shift has occurred, cannot be explained only by the biogeographic affinity of the species, and the fisheries impact and management strategies could be considered important forces to structure larval fish communities.

B. bathymaster is the most abundant fish larvae species in the tropical Mexican Pacific (Franco-Gordo et al. 2001b) and is scarce in California Current zone (Moser et al. 1993). The small size of *Bregmaceros* as adults (ca 12 cm) make them unattractive for fisheries, however has been described as ecologically relevant in the oceanic food webs (Zavala-García & Flores-Coto, 1994). It is considered as a tropical affinity species and the adults occur mainly in oceanic waters (Norcross & Shaw, 1984), however the larvae are more abundant at inshore waters, and response positively to UI and negatively to MEI. Apparently the general rule in both tropical and temperate regions could be that the conditions associated to cool waters generally are associated with increased zooplankton production that would promote higher larval fish production and survival (Smith & Moser, 2003).

Table 5. Zooplankton studies of El Niño event in the Pacific Northwest.

Source	Period	Study area	Variable	Conspicuous features	Tropicalization
Gómez-Gutierrez et al. (1995)	1986-1987	West coast of Baja California	Euphausiids	A high proportion of species endemic from tropical and equatorial eastern Pacific. Temperate euphausiids, like *Euphausia pacifica*, could displace their reproductive areas because there was no evidence of recent reproduction.	Yes. Tropical assemblages found in October 1987 (the most northern distribution recorded). It is associated to a warming of water masses.
Funes-Rodríguez et al. (1998)	1958-1959 1983-1984	West coast of Baja California South	Fish larvae	The larvae of tropical species were abundant around Punta Eugenia, related to the influence of warm waters during El Niño periods. The distributions of larvae of *Opistonema* sp., *Benthosema panamense* and *Auxis* spp. showed significant range extensions.	Yes. Presence of tropical species such as *Etremeus teres*, *Vinciguerria lucetia*, *Diogenichthys laternatus* and others.
Mullin (1998)	1950-1997	California Current	Zooplankton Copepods	Cold water calanoid copepods dominant in the California Current showed similar abundances in spring and winter in comparable samples from pre-1970 and post-1978. However, there were reductions of 58-91% in the abundance during El Niño periods.	No. Only reductions of *Calanus pacificus*, a cold-water specie.
Lavaniegos et al. (2002)	1997-1999	Western coast Peninsula of California	Chlorophyll *a* zooplankton	Chl a increased in La Niña and near-surface chl *a* was high, with differences between Baja California and southern California regions. Zooplankton biomass during the ENSO period was low. In La Niña macrozooplankton volume increase.	Yes. High abundances of salps, which showed an affinity for warm saline water masses.
Mackas & Galbraith (2002)	1996-1999	Southern British Columbia (oceanic waters)	Zooplankton biomass and community composition	Lower total biomass and shifts in community composition. Appeared taxa endemic of the southern part of California Current. El Niño associated changes in the zooplankton community were more apparent over the shelf-break and slope, and weaker further offshore.	Yes. Reduced abundance of endemic boreal temperate species. Presence of *Nyctiphanes simplex*.
Marinovic et al. (2002)	1997-1999	Monterrey Bay	Zooplankton Euphausiids	Abundance decreased dramatically in summer 1997. Cold water species *Eufausia pacifica* and *Thysanoessa spinifera* decreased. Zooplankton and euphausiid abundance and composition returned gradually to a typical state in 1998.	Yes. Presence of *Nyctiphanes simplex*, a southern latitude species..
Sánchez-Velasco et al. (2000)	1997-1998	Gulf of California	Fish larvae Zooplankton	High values of zooplancton biomass and *Engraulis mordax* during and after the El Niño. Both groups concentrated close to isla Angel de la Guarda and Isla Tiburon, the coldest zone.	No data.

Avalos-García et al. (2003)	1997-1998	Gulf of California	Larval fish	Low larval abundance of cold water species like *Sardinops sagax* and *Scomber japonicus*. The El Niño 1997-1998 conditions were more favorable for tropical and subtropical species.	Yes. High abundance of *Benthosema panamense* could be due to ocean warning.
Brinton & Townsend (2003)	1950-2002	Southern California Current	Euphausiids	*Euphausia pacifica* and *Nematoscelis difficilis*, the most dominant cold water species during 1950-2002, decreased during El Niño events. Subtropical species like: *E. eximia*, *E. gibboides*, and *E. recurva*, were present in small numbers, most notably during El Niño events.	Yes. A tropical species such: *E. distinguenda*, *E. tenera*, *E. lamelligera* and *E. diomedae*, were recorded during 1998, the only time in tle 52 yr of survey.
Funes-Rodríguez et al. (2003)	1982-2000	West coast of Baja California	Mesopelagic fish larvae	The structure and density is controlled to a large extend by the seasonal environmental dynamics, however the larval assemblages show changes associated with El Niño warning event the south area and with seasonality in the northern area.	Yes. High abundances of warm-water species such *Vinciguerria lucetia*, *Opistonema* spp. and *Benthosema panamense*
Lavaniegos et al., 2003	1997-1998	Western coast Peninsula of California	Chlorophyll Zooplankton Salps Copepods	Regional differences in zooplankton biomass. In some coastal points the chlorophyll remained constant. Changes in species composition of zooplankton affect the biomass values, and these changes were due to the increase of tropical species.	Yes. Largest values of salps and small tropical copepods.
Lavaniegos & Ohman (2003)	1951-2002	Southern California Current	Tunicates	Evidence for ecosystem change between El Niño 1976-1977 and 1998-1999. However no clear long-term patterns respect to El Niño, as both total salp biomass and that of individual species decreased in some El Niño years and increased in others.	Yes. The rarer subtropical *Doliolum denticulatum* was present predominantly during the warm phase.
Smith & Moser (2003)	1951-2003	California Current	Fish larvae	Mesopelagic larvae of the southern offshore species had the greatest response to the regime shift of 1976-77. Cool water conditions are generally associated with increased zooplankton production which would suggest higher larval fish production and survival.	Yes. *Vinciguerria lucetia* showed a near two-fold increase. It was the most abundand larva in the southern California Bight.

7.5 References

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Capítulo 8

Interannual variability of the diversity and structure of ichthyoplankton assemblages in the central Mexican Pacific.

Franco-Gordo, C. Godínez-Domínguez, E. & Freire, J. Manuscrito sometido. *Progress in Oceanography.*

Interannual variability of the diversity and structure of ichthyoplankton assemblages in the central Mexican Pacific

ABSTRACT

We examined larval fish diversity and assemblage structure on the central Mexican Pacific (coast of Jalisco and Colima) using data from samplings carried out with a Bongo net at 12 stations during 27 months, from December 1995 through December 1998. A total of 132 taxa were recorded, and the dominant species were *Bregmaceros bathymaster* (90% of the total abundance), *Dormitator latifrons* (1.9%) and *Harengula thrissina* (0.8%). Only *B. bathymaster*, *D. latifrons* and *Gobionellus* sp. attained the 100 % of occurrence. The effects of the 1997-98 El Niño event in ichthyoplankton diversity were significant, however the prevalence of the normal seasonality could be observed. Diversity null models were used to determine structural changes in the assemblage due to El Niño effects; both species richness and evenness were highest during El Niño. The most parsimonious models of assemblage organization include the El Niño and seasonality as most significant environmental variability sources. The small-scale spatial variability expressed as the cross-shore gradient was not relevant. The dominant species group formed by *B. bathymaster*, *D. latifrons*, and *Vinciguerria lucetia* typify for similarity both the previous and El Niño period and the only change was the abundance difference among periods. The El Niño period was typified

by the dominant species *Bentosema panamense* and *H. thrissina*, and by the rare species *Euthynus lineatus,* and species of the genus *Lujtanus*. The assemblage shows a similar organization in the different seasons, sharing the same dominant species group. Seasonality produces only changes in the abundances and relative frequencies of dominant species and different rare species are characteristic of the different seasons. The average taxonomical distinctness, that could be considered as a measure of functional diversity, was highly sensitive to the seasonal change of the assemblages independently of the El Niño; this index showed lowest values during tropical and transition periods characterized by warm and oligotrophic waters.

Key words: El Niño Southern Oscillation, fish larvae, diversity null models, taxonomical distinctness, species richness, evenness, assemblages, tropical Pacific.

8.1 Introducction

The El Niño events are the most important interannual source of environmental variability in the Pacific Ocean and their impacts and consequences on marine ecosystems and ecological processes are still being surveyed. A large knowledge base has been cumulated about the pelagic habitat and the primary and secondary production in equatorial, subtropical and temperate areas of the north Pacific (Bograd and Lynn, 2001; Chavez et al., 1999; 2002; Fiedler, 2002),

which has allowed characterising the main direct effects of El Niño events. However, many gaps remain about the knowledge of the middle- and long-term effects on larval and postlarval fish populations and communities in coastal tropical waters.

During ENSO events four main responses could be observed in the pelagic habitats: 1) a physical-biological coupling; the decrease in the availability of nutrients produce an immediate response of phytoplankton and zooplanktic biomass (Bograd and Lynn 2001; Chavez et al. 1999; 2002); 2) evidence of the prevalence of an attenuated seasonal signal in the environment and the planktic communities (Chavez et al. 2002; Franco-Gordo et al. in review); 3) a differential response along the cross-shore gradient, the nearshore zone shows higher productivity levels than deep zones and support the highest plankton densities (Chavez et al. 2002; Franco-Gordo et al., in review); and 4) changes in the species composition that could be found in practically all plankton groups. A tropicalization of the plankton has been reported in subtropical and temperate areas of the Pacific Northwest (Gómez-Gutierrez et al., 1995, Funes-Rodríguez et al., 1998; Lavaniegos et al., 2002; Mackas and Galbraith, 2002; Marinovich et al., 2002; Avalos-Garcia et al., 2003; Brinton and Townsend, 2003; Lavaniegos et al., 2003; Lavaniegos and Ohman, 2003; Smith and Moser et al., 2003).

The relationships between larval fish assemblages in the Pacific Ocean and hydrographic features have been documented in a wide

range of systems (e. g. Avalos-Garcia et al., 2003; Doyle, et al. 1993; Franco-Gordo et al. 2002; 2003; Funes-Rodriguez et al., 1998; Miller et al., 1985; Moser and Smith, 1993; Sanchez-Velasco et al., 2000; Smith and Moser, 2003). Larval assemblages have been further explained as the result of convergent spawning strategies among members of a given postlarval assemblage (e. g. Sherman et al., 1984; Doyle et al, 1993). However few studies have reported analytical procedures to weight the importance of the environmental factors, and the potential hierarchies among the several sources of variability have not been formally approached.

Diversity estimation and ordination of assemblages are the methods most frequently used in community analysis to identify conspicuous features of the ecosystems and the underlying ecological processes. In the marine environment, there exists little empirical information on the relationship between marine diversity, stability and resilience (Allison et al., 1996). In ichthyoplankton communities, diversity is a valuable index that has been used to evaluate temporal or spatial variations in the species composition and to infer environmental changes. This is particularly relevant in a zone, as the central Mexican Pacific, with a high variability at several temporal scales that affect coastal processes and, as a consequence, the spatial patterns of larval fish (Franco-Gordo et al. in review).

In the central Mexican Pacific, the plankton community shows a markedly seasonal response in the spatial distribution of the primary

production, zooplanktic biomass and larval fish abundance (Franco-Gordo et al 2001a; b), and larval fish assemblages (Franco-Gordo et al., 2002). During the 1997-98 El Niño event the normal patterns of zooplanktic biomass and larval fish abundance cited above were decoupled (Franco-Gordo et al., in review). An attenuated seasonal signal was recorded while the spatial distribution pattern disappeared. Here we analyse the interannual variability of the most conspicuous structural features of the larval fish communities. Diversity and assemblage structure are scale-dependent processes, and for this reason we analyse the longest available series of larval fish abundances in the central Mexican Pacific to test a set of hypotheses about the temporal and spatial organization of the larval fish communities. In this work we hypothesize that temporal oceanographic and climatic processes, as normal seasonality and the ENSO event (1997-1998), are reflected in the ichthyoplankton community structure and spatial distribution.

8.2 Study area

The surveyed area comprises a fringe along the continental shelf off the coasts of Jalisco and Colima, central portion of the Mexican Pacific located between Punta Farallón, in Jalisco (19°19'77"N, 105°00'28"W), and Cuyutlán, Colima (18°58'24"N, 104°13'51"W) (Fig. 1). The continental shelf is narrow, comprising, up to the 200 m isobaths, only 7-10 km (Filonov et al., 2000).

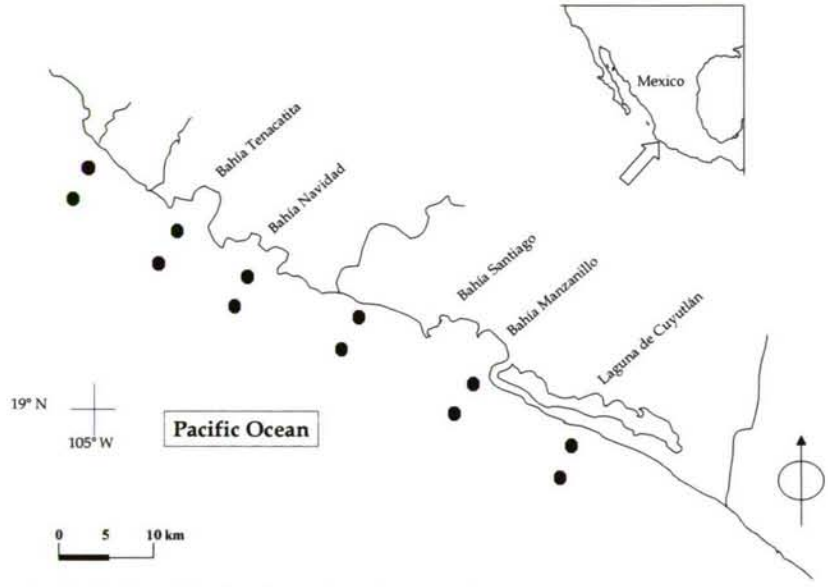


Figure 1. Study area, dots indicate the zooplanplankton sampling sites

The general hydrography of the study area is described by Wyrtky (1965) for the eastern Pacific Ocean and is characterized by a northeastward flow during summertime and southwestward in winter. The surface layer is formed by a seasonal, variable mixture of tropical surface water, and water from the California Current (CC). In winter and spring the area is influenced mainly by CC that is mixed with the Equatorial Countercurrent and the North Equatorial Current between 15°N and 20°N. In summer and autumn, the CC is weakened and the area is affected mainly by the northward flow of the tropical waters transported by the Equatorial Countercurrent through the North Equatorial Current and the Costa Rica Coastal Current (Pacheco-Sandoval, 1991; Wyrtky, 1965). In Jalisco and Colima coast the

current patterns are defined by two main phases: The first one is influenced by the CC, the cool waters affect the area from January to May; the second phase characterized by a tropical water mass from the North Equatorial Countercurrent is present for the period July to November, a third phase is determined by the transition between both previous phases, characterized by a non-defined conditions in June and December. These environmental patterns determine the seasonal variability in the coastal ecosystem in the study area and affect the primary production (Franco-Gordo et al., in review) zooplanktic biomass and larval fish abundance (Franco-Gordo et al 2001), and larval fish assemblages and diversity (Franco-Gordo et al., 2002; 2003).

8.3 Material and methods

8.3.1 Samplings

The area was surveyed using a 12-station plan on board the BIP-V oceanographic vessel (Fig. 1) exclusively over the continental shelf. Zooplankton samplings were carried out monthly at night (20:00 to 07:00 h) from December 1995 through December 1998. No samplings were made in some months due to adverse climatic conditions or problems with the vessel. Zooplankton tows were performed following Smith and Richardson (1977). Samples were collected by means of a Bongo net with a 0.505 mm mesh size. This gear was hauled obliquely and the net was sent down tried to cover

the most water column. A digital flowmeter was adapted to the net mouth in order to estimate the amount of water filtered. Previously to each tow, a profile of temperature and salinity was recorded using a CTD profiler SBE-19. Abundance data were standardized into number of larvae per 10 m^2 (Smith & Richardson, 1977).

8.3.2 Diversity

Diversity was analytically decomposed in its components using estimates of richness, evenness, and taxonomical distinctness. Species richness and evenness were estimated using two null models (Gotelli and Graves 1996, Gotelli and Entsminger 2001): rarefaction curves and the probability of an interspecific encounter (PIE). Data were pooled by cruise and depth strata and monthly estimates of diversity were obtained. In both rarefaction and PIE the calculus procedure employed the Monte Carlo method to generate mean and a confidence interval (95%) of diversity estimates. Several zooplankton studies have reported that the species assemblages during El Niño events are strongly recomposed and other species with different biogeographical affinities replace to the local communities. These make that a simple diversity index could be unable to detect the community changes, being necessary other diversity indexes such as those based on taxonomical relations. The taxonomical distinctness has been proposed as a biodiversity index based on taxonomic (or phylogenetic) relatedness patterns within an assemblage (Clarke and Warwick 2001a), and is estimated by the

average taxonomic distinctness and the variation in taxonomic distinctness. The average taxonomic distinctness (AvTD) is the average path length between every pair of species traced through a taxonomic tree:

$$\Delta^+ = \left[\sum\sum_{i<j} \omega_{ij} \right] / \left[s(s-1)/2 \right]$$

where s is the number of species present, the double summation is over the set (i = 1,....., s; j = 1, ..., s, such that $i < j$), and w_{ij} is the distinctness weight between species i and j. The taxonomic levels considered for us were from species to order. The variation in taxonomic distinctness (VarTD) is defined as:

$$\Lambda^+ = \left[\sum\sum_{i\neq j} (\omega_{ij} - \varpi)^2 \right] / \left[s(s-1) \right]$$

Monthly estimates of both taxonomic distinctness indices by depth strata were obtained using pooled abundance-species data and the software Primer v5 (Clarke and Warwick, 2001b). To determine the influence of both seasonal and interannual source of variability in

taxonomical distinctness measures (AvTD and VarTD) a two-way ANOVA was carried out.

The diversity estimates employed here are considered robust to abundance and effort biases (see Gotelli and Graves 1996; Clarke and Warwick 2001a). However, the Lambda index is not exactly unbiased as sample size changes Clarke and Warwick (2001a) but the bias is very small and could be not relevant.

Generalized linear models (GLM) were used to analyse the spatial and temporal patterns of the diversity components and their relationships with the environmental variables. The following environmental variables were used:

-Inshore and offshore sea surface temperature (SST) and salinity.

-The Multivariate ENSO Index MEI (Wolter & Timlin, 1993; 1998) as an indicator of El Niño/La Niña conditions in the tropical Pacific. The MEI is based on six highly correlated observed variables in the tropical Pacific: SST, atmospheric sea level, pressure (SLP), surface winds, zonal and meridional surface air temperature and total cloudiness. (Details on the computation of the MEI are available at: http://www.cdc.noaa.gov/~kew/MEI/mei.htlm).

-The upwelling index (UI) at 21° N (available at http://www.pfeg.noaa.gov).

8.3.2 Assemblage structure

We assume that the seasonality and interannual events as El Niño are the most influent temporal sources of variability in the pelagic habitat in the study area, whereas cross-shelf variability defines the main spatial gradient. A set of *a priori* hypotheses were designed to test a wide range of multivariate models of increasing complexity to explain assemblage structure variability in relation with environmental variables (seasonality, El Niño event and cross-shore distance). Three groups of models are considered: the first group include the full model (all the single variables and interactions) and models constructed removing one interaction in each step (the order was based in the factor weight). The second group (basic models) include only one single variable by model, and the third (other model) are constructed following the single factor weight including the highest factors.

The method consists in the use of canonical correspondence analysis (CCA) to measure the fit of model to data, and the use of a selection model procedure to determine the best model. Multivariate model selection, using the principle of parsimony and the hierarchical relation among the environmental factors explaining spatial and temporal variability of the ichthyoplankton community, were carried out following the procedure proposed by Godínez-Domínguez and Freire (2003). The method use the Akaike information criterion (AIC):

$$AIC = -2\log\left[\ell\left(\hat{\theta}\right)\right] + 2K$$

where k = the number of parameters. Simple transformations of the estimated residual sum of squares (RSS) allow obtaining the value of log $[\mathscr{L}(\theta)]$ using least-squares estimation with normally distributed errors rather than the likelihood method. For all standard linear models, we can take

$$\log\left[\mathscr{L}\left(\hat{\theta}\right)\right] = -\frac{1}{2} n \log(\hat{\sigma}^2)$$

where log = $\log_e$, n is sample size and σ^2 = RSS/n. The trace obtained by each model using the canonical correspondence analysis (CCA) (ter Braak and Smilauer 2002) was employed to estimate the residual sum of squares (RSS):

$$\mathrm{RSS} = (\text{ sum of all eigenvalues}) - \sum_{i=1}^{h} \mathrm{trace}_i$$

Partial canonical correspondence analysis (Borcard et al. 1992) was carried out to determine the individual weight of the spatial and temporal factors and their interactions. The procedure described above allows to determine the most parsimonious model however the variance decomposition allow us to quantify the weight of the

variables (single variables and interactions of them) employed in the fitted models.

Non-metric multidimensional scaling (MDS) (Clarke and Warwick 2001b) was used to explore visually the ordination patterns of the most parsimonious models. The species assemblages that typify to the most parsimonious spatial-temporal models were determined by similarity-dissimilarity rank using the SIMPER procedure (Clarke and Warwick 2001b). Bray-Curtis index and four-root transformation were used for both MDS and similarity-dissimilarity analyses.

8.4 Results

The relative abundance of the 132 taxa sampled off Jalisco and Colima during 1995-1998 is shown in Table 1. *Bregmaceros bathymaster* was the dominant species in the assemblage representing 90.4% of the total number of larvae, whereas the following taxa showed low relative abundances, as *Dormitator latifrons* (1.9%), *Harengula thrissina* (0.9%), and Engraulidae (0.85%). This pattern of relative abundance shows clearly an uneven structure of the assemblage. *B. bathymaster, D. latifrons* and *Gobionellus* sp. were the only taxa that appeared in all the samples.

Table 1. Summary of the abundance and occurrence of the larval fish taxa found in the central Mexican Pacific during the 1995-1998 period. Taxa are sorted by mean abundance (organisms / 10 m2).

		Mean abundance	% of the total count	Cummulative percentage	Monthly abundance range % minimum	% maximum	Frequency of occurrence
1	*Bregmaceros bathymaster*	15948.1	90.43	90.43	1.984	98.42	100.00
2	*Dormitator latifrons*	332.9	1.89	92.32	0.229	11.31	100.00
3	*Harengula thrissina*	150.3	0.85	93.17	0.040	42.06	59.26
4	Engraulidae	149.1	0.85	94.01	0.017	38.72	62.96
5	*Vinciguerria lucetia*	120.4	0.68	94.70	0.015	25.74	85.19
6	*Euthynus lineatus*	110.5	0.63	95.32	0.006	22.63	66.67
7	*Benthosema panamense*	96.8	0.55	95.87	0.007	7.67	74.07
8	Sciaenidae	84.7	0.48	96.35	0.030	3.42	62.96
9	*Gobionellus* sp.	78.4	0.44	96.80	0.039	3.53	100.00
10	Gobiidae	66.5	0.38	97.17	0.012	6.85	96.30
11	*Syacium ovale*	33.2	0.19	97.36	0.008	2.49	88.89
12	Pomacentridae	32.7	0.19	97.55	0.030	5.34	51.85
13	*Lutjanus* spp.	26.8	0.15	97.70	0.024	18.67	25.93
14	*Lutjanus argentiventris*	25.7	0.15	97.85	0.024	18.40	29.63
15	*Auxis* sp.	25.0	0.14	97.99	0.016	4.66	74.07
16	*Lutjanus novemfaciatus*	23.6	0.13	98.12	0.025	9.47	29.63
17	*Symphurus elongatus*	20.3	0.12	98.24	0.004	0.76	48.15
18	*Caranx caballus*	19.4	0.11	98.35	0.004	5.17	51.85
19	*Cetengraulis mysticetus*	16.6	0.09	98.44	0.016	0.73	18.52
20	*Xyrichtys* sp.	15.9	0.09	98.53	0.009	0.85	85.19
21	*Sphoeroides annulatus*	15.5	0.09	98.62	0.017	1.01	51.85
22	Eleotridae	14.9	0.08	98.70	0.015	2.71	29.63
23	*Opistonema* sp.	11.3	0.06	98.77	0.016	0.17	22.22
24	*Synodus sechurae*	10.8	0.06	98.83	0.005	2.81	51.85
25	*Engraulis* sp.	9.5	0.05	98.88	0.850	17.50	7.41
26	*Cubiceps pauciradiatus*	9.1	0.05	98.93	0.025	1.64	48.15
27	*Lutjanus guttatus*	9.0	0.05	98.98	0.035	3.82	29.63

8.4.1 Diversity

During El Niño period the species richness was slightly higher than during the previous normal period in both offshore and inshore zones. The evenness index (PIE) showed an important increase during El Niño period and its variance decreased (Fig. 2). The seasonal pattern of diversity was prevalent both during El Niño and non-El Niño, but the main scale of temporal variability was interannual related to the ENSO events. The lowest diversity values were obtained during the

period when the colder, more productive California Current flows along this coast southward from higher latitudes. These conditions produce decreases in diversity and allow the dominance of one or a few species.

The average taxonomic distinctness index (AvTD) did not show interannuall patterns (ENSO effect) neither inshore nor offshore (Fig. 3). However lowest values of months corresponding to tropical period (July to November) and transition (December and June), and the anova results corroborate this statement (Table 2). The variation of taxonomical distinctness (VarTD) was in general larger than expected and this result could represent a widespread of higher taxa or taxonomic richness during the normal periods and during El Niño (Fig. 3).

The generalized linear models GLMs (Table 3) confirm that the El Niño event was the most important source of temporal variability of the diversity. The multivariate ENSO index (MEI) and sea surface temperature (SST) were the main factors included in the models fitted for richness and evenness.

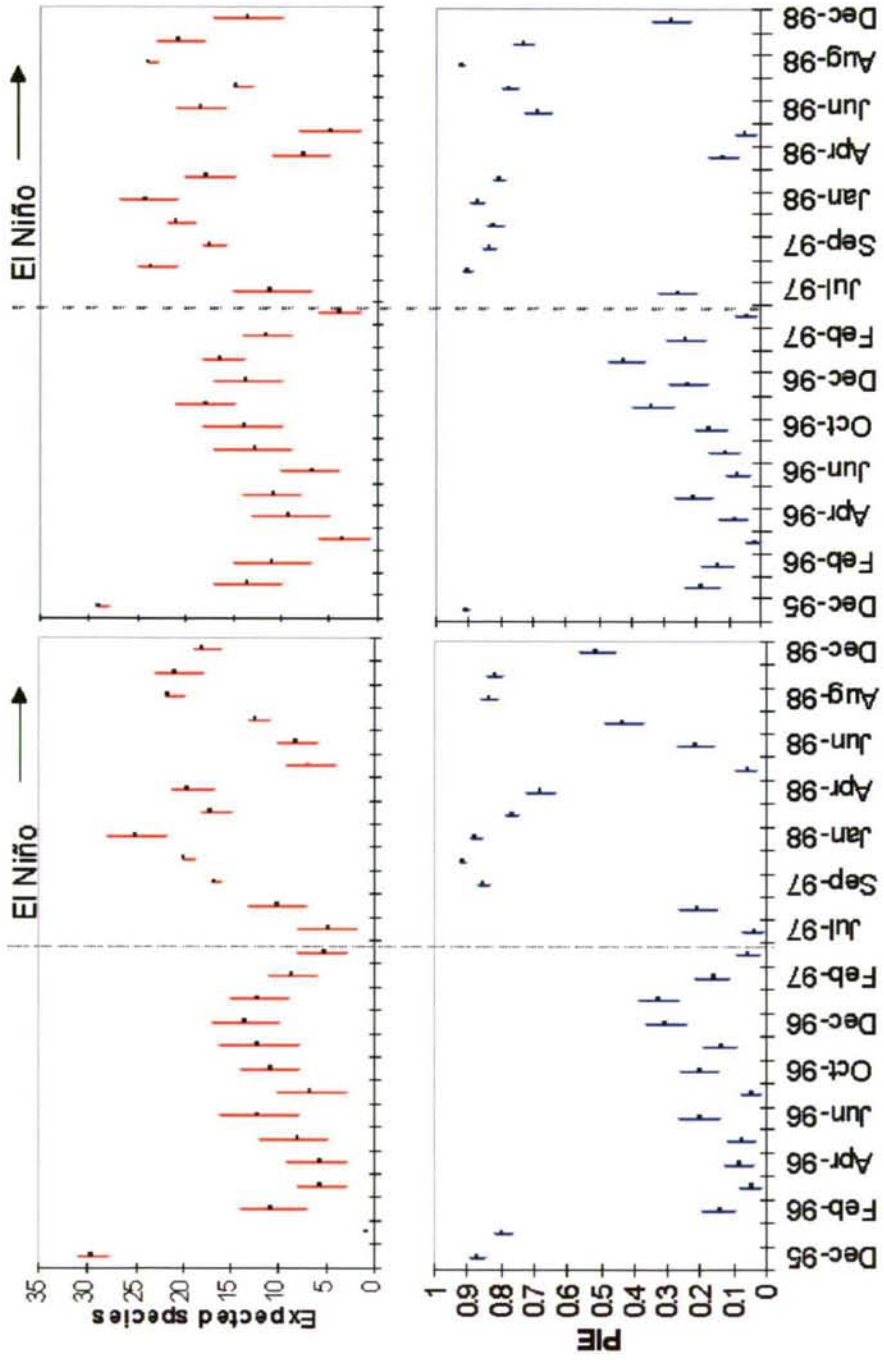


Figure 2. Temporal distribution of the species richness and evenness (PIE) of the larval fish assemblages of the central Mexican Pacific (mean and 95% confidence intervals are showed.

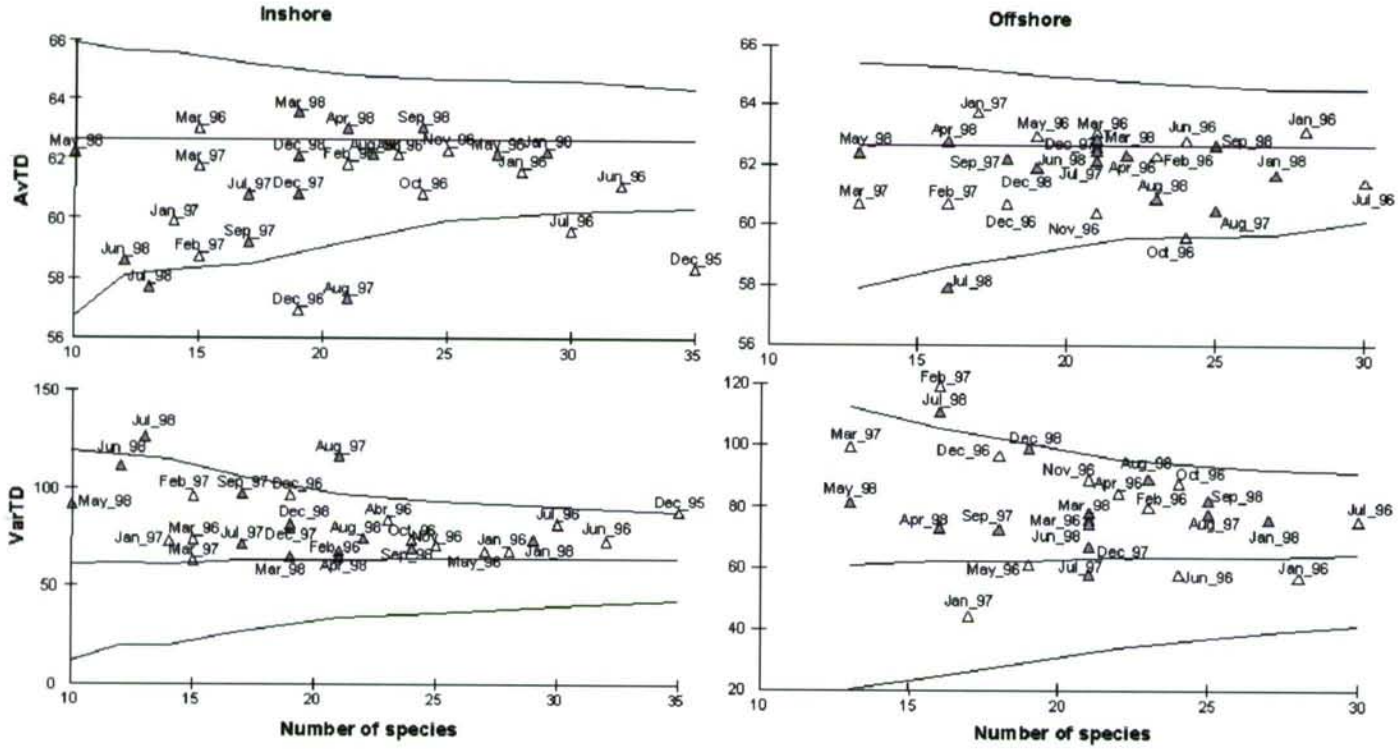


Figure 3. Average (AvTD) and variation of taxonomic distinctness (VarTD) of larval fish assemblage in the inshore and offshore zones. Filed triangles represent the monthly values of El Niño period. Lines represent the 95% probability funnels.

Table 2. Results of two-way ANOVAs to test the effects of seasonality and El Niño in the the average taxonomic distinctness (AvTD) and the variation of taxonomic distinctness (VarTD).

Average taxonomic distinctness

Effect	d.f.	F-value	*p*
Season	2	6.29	0.003
El Niño	1	2.05	0.158
season*El Niño	2	0.87	0.427
error	47		

Variation of taxonomic distinctness

Effect	d.f.	F-value	*p*
Season	2	1.35	0.268
El Niño	1	0.46	0.502
season*El Niño	2	0.24	0.790
error	47		

Table 3. Generalized linear models (GLM) fitted to diversity components following the AIC to select the most parsimonious model. MEI (Multivariate ENSO index), SST (sea surface temperature), UI (upwelling index). The value of the parameters included in the most parsimonious models are showed.

	MEI	SST	UI	Season	d.f.	AIC	*p*
Richness inshore	0.959				1	149.77	0.314
Richness offshore		1.750			1	134.07	0.001
PIE inshore	0.107				1	13.81	0.047
PIE offshore	0.084	0.087			2	11.01	0.007

Table 4. Results of the procedure for selection of the most parsimonious model of assemblage structure using the Akaike information criterion. (a) The models are detailed (X idicate the variable or parameter include in the model). (b) Results of CCA and the permutation test of the fitted models, and the ranking of the models estimated using AIC.

a		Full model	Basic models plus interactions				Basic models				Other models			Factor weight
Distance	Inshore	x	x	x	x	x	x			x				0.015
ENSO	El Niño	x	x	x	x	x	x		x		x	x	x	0.148
Season	Califonia Current	x	x	x	x	x	x	x			x	x	x	*0.154
	Tropical	x	x	x	x	x	x	x			x	x	x	
Interactions	ENSO*Calif. Current	x	x	x	x	x					x	x		0.026
	ENSO*Tropical	x	x	x	x						x	x		0.057
	ENSO*Inshore	x	x	x							x			0.016
	Inshore*Calif. Current	x	x								x			0.017
	Inshore*Tropical	x									x			0.017
b														
	Sum of all canonical eigenvalues	0.441	0.433	0.416	0.4	0.343	0.317	0.153	0.147	0.015	0.435	0.385	0.302	
	K (parameters number)	9	8	7	6	5	4	2	1	1	8	5	3	
	P-value 1st canonical Axis	0.008	0.002	0.002	0.002	0.002	0.002	0.02			0.002	0.002	0.002	
	P-value all canonical Axis	0.16	0.09	0.05	0.02	0.01	0.012	0.05	0.004	0.9	0.09	0.006	0.006	
	AICc	-161.684	-164.696	-166.837	-170.115	-169.352	-171.389	-170.829	-172.786	-168.703	-165.987	-171.651	-173.155	
	w_i	0.001	0.004	0.012	0.061	0.042	0.115	0.087	0.231	0.030	0.008	0.131	0.278	
	model ranking	12	11	9	6	7	4	5	2	8	10	3	1	

* the factor weight include the explained variance of both seasons: CC period and tropical period

Table 5. Percentage contribution of typifying species similarity within seasonal groups of the larval fish assemblages of the central Mexican Pacific. Only species up to 90% of the cummulative similarity are showed.

	Califor. Current Jan-May 1996	Tropical Jul-Nov 1996	Califor. Current Jan-May 1997	Tropical Jul-Nov 1997	Califor. Current Jan-May 1998	Tropical Jul-Nov 1998
Bregmaceros bathymaster	97.8	86.9	96.4	16.3	84.5	19.0
Dormitator latifrons		3.3		16.1	6.5	2.3
Harengula thrissina				24.2		
Euthynus lineatus				10.8		10.2
Vinciguerria lucetia				5.5		4.1
Benthosema panamense				3.2		
Lutjanus novemfaciatus				10.6		
Gobionellus sp.				3.1		2.0
Gobiidae				1.7		9.7
Lutjanus spp						15.4
Lutjanus argentiventris						15.1
Engraulidae						11.8
Pomacentridae						2.3

8.4.2 Assemblages

The most parsimonious model explaining the assemblage organization includes the ENSO event and seasonality, the second best model only include the ENSO event and the third best model include ENSO, seasonality and the interaction among them (Table 4). The parsimony is rooted in the concept of simplicity and considers only the minimum number of parameters or variables to explain a phenomenon. In this case, the best model only included seasonality and ENSO events to explain the variability of the larval fish assemblages, (figure 4) and posterior increases in the number of parameters in the model could add more complexity than information. The rank of models obtained by the procedure employed can be understood as a hierarchy of the models and implicitly as a hierarchy of environmental factors. The variance decomposition shows the single weight of the variables considered as the environmental variability. Season is the variable that more variance explains followed by ENSO, however season has three possible states (CC, tropical and transition) while ENSO only two (normal and ENSO period) and these is taken in account by the Akaike procedure. The spatial variability, expressed as inshore-offshore gradient is not considered as an important factor in the assemblage organization, and factors as interactions between ENSO and season, showed highest values of explained variance (see table 4).

8.4.3 Seasonal assemblage organization

The highest similarity of the species that typify the seasons of the period previous to the El Niño event reflect a high dominance of *B. bathymaster*. CC period of 1996, tropical 1996 and CC in 1997, with values of similarity of 98, 87 and 96% respectively (Table 5). The tropical seasons during El Niño period (Jul-Nov 1997 and 1998) showed more even similarity values. *B. bathymaster* was also during El Niño the dominant species, and only during the tropical period of 1997 *Harengula thrissina* recorded a highest similarity value.

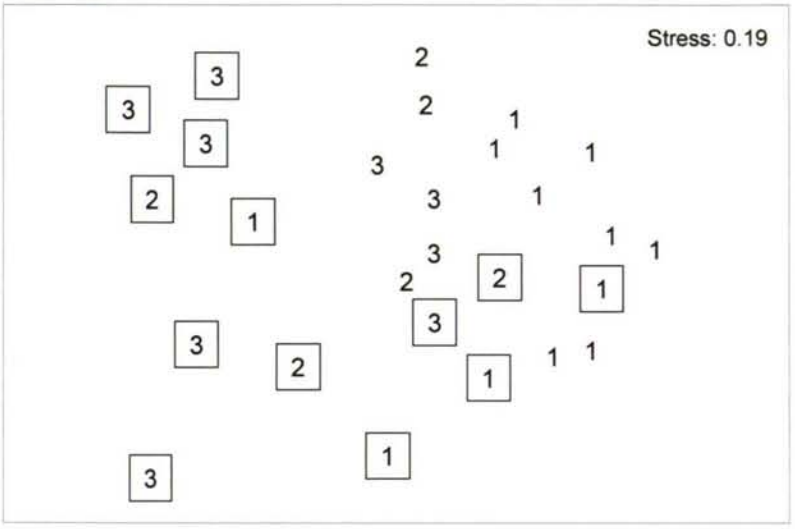
8.4.4 Interannual assemblage organization

Similar species typified for similarity the assemblages for the normal and El Niño periods (*B. bathymaster, D. latifrons*, *Gobionellus* sp. Gobidae and *Vinciguerria lucetia*) (Table 6). The species that typify to dissimilarity are *B. bathymaster Sciaenidae, H. thrissina*, Engraulidae *Euthynus lineatus* and *Bentosema panamense*. *B. bathymaster* typifies for both similarity and dissimilarity of the community and this feature is due to the abundance differences between periods. Sciaenidae taxa and *Symphurus elongatus* and *Sympurus atramentatus* showed affinity for the normal period while *H. thrissina, E. lineatus, B. panamense*, and species of *Lutjanus* genus showed affinity for El Niño period.

Table 6. Percentage contribution of typifying species similarity within the discriminated species groups and disimilarity within interannual periods

Similarity				Disimilarity
	Previous El Niño	El Niño		between groups
Bregmaceros bathymaster	25.79	13.75	*Bregmaceros bathymaster*	7.78
Dormitator latifrons	10.18	10.77	Sciaenidae	2.88
Gobionellus sp.	6.29	6.85	*Harengula thrissina*	2.65
Sciaenidae	5.15		Engraulidae	2.64
Gobiidae	4.67	7.88	*Euthynus lineatus*	2.56
Xyrichtys sp.	4.43	2.58	*Benthosema panamense*	2.44
Vinciguerria lucetia	3.64	5.91	*Vinciguerria lucetia*	1.93
Syacium ovale	3.19	5.81	*Lutjanus* spp	1.9
Symphurus atramentatus	2.16		Pomacentridae	1.82
Engraulidae	2.07	3.32	*Lutjanus argentiventris*	1.73
Auxis sp.	2.02		*Symphurus elongatus*	1.71
Symphurus chabanaudi	1.83		*Caranx caballus*	1.69
Benthosema panamense	1.65	5.77	*Symphurus atramentatus*	1.64
Symphurus elongatus	1.61		*Lutjanus novemfaciatus*	1.58
Pomacentridae	1.52		*Gobiesox* sp.	1.54
Chloroscombrus orqueta	1.49		*Symphurus chabanaudi*	1.49
Euthynus lineatus	1.48	4.88	*Sphoeroides annulatus*	1.47
Etropus crossotus	1.44		*Cubiceps pauciradiatus*	1.45
Halichoeres dispilus	1.34		*Synodus sechurae*	1.42
Moringuidae	1.22		*Auxis* sp.	1.41
Synodus sechurae	1.17		*Chloroscombrus orqueta*	1.37
Harengula thrissina	1.14	3.5	*Halichoeres dispilus*	1.31
Caranx sexfasciatus	0.88		Eleotridae	1.31
Abudefduf troschelli	0.86		*Syacium ovale*	1.29
Labrisomus multiporosus	0.86		*Mugil cephalus*	1.22
Ophidion sp.	0.86		*Etropus crossotus*	1.21
Mugil cephalus	0.76	1.35	Moringuidae	1.2
Eleotridae	0.67		*Abudefduf troschelli*	1.19
Auxis sp.		3.2	*Labrisomus multiporosus*	1.19
Gobiesox sp.		2.58	*Lutjanus guttatus*	1.19
Cubiceps pauciradiatus		2.24	*Xyrichtys* sp.	1.16
Caranx caballus		2.17	*Dormitator latifrons*	1.15
Lutjanus spp		1.99	*Caranx sexfasciatus*	1.15
Sphoeroides annulatus		1.9	*Cetengraulis mysticetus*	1.13
Lutjanus argentiventris		1.54		
Pomacentridae		1.28		
Lutjanus novemfaciatus		1.06		

Inshore



Offshore

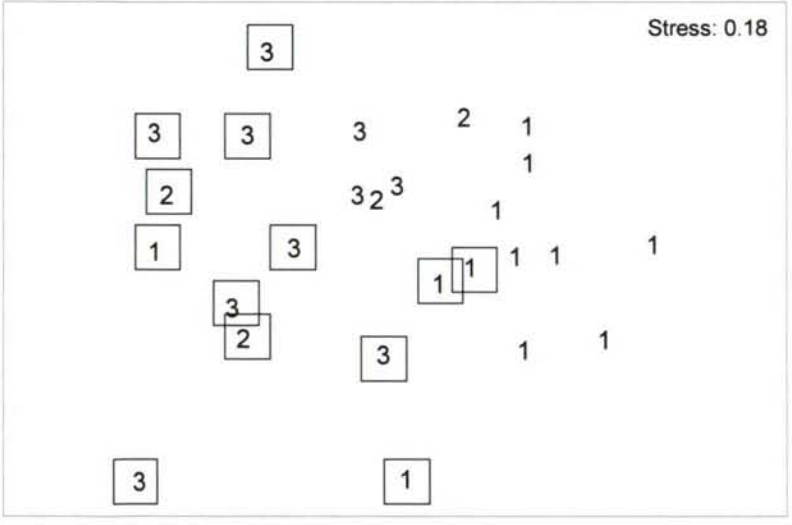


Figure 4. Ordination patterns using non-parametric multidimensional scaling (nMDS) of the larval fish assemblages of the Mexican central Pacific. 1 = CC period, 2 = transition, 3 = tropical period. Numbers with frames are the months of El Niño period.

8.5 Discussion

Different processes related to spawning, oceanography and larval life histories affect the composition and distribution of the larval fish communities (Mullin, 1993), and during the El Niño these three aspects could be altered. The convergence of spawning strategies observed in fish communities (Dayle et al., 1993) could be due to the common goal of increasing the survival by coupling spawning with production processes and circulation-retention patterns (Parrish et al., 1981; Iles and Sinclair, 1982; Frank and Leggett, 1983; Werner et al, 1999; Winemiller and Rose 1992). In the central Mexican Pacific the peaks in the larval fish abundance coincide with primary and secondary production patterns and reproductive seasonality of the fish community (Franco-Gordo et al., 2001a; b; in review), corroborating that the spawning strategies in fish populations have evolved in synchrony with prevailing oceanographic processes. However during El Niño event, spawning patterns, food availability and transport mechanisms could be modified and decoupled, and as a consequence the larval fish survival could decrease.

There are few studies available about the effect of the El Niño event on the spawning activity in fish communities of the tropical zones, or the differential responses of some fish populations. It is possible to assume that the environmental stress reduces in a different way the reproductive activity of different species, and by the other hand it is possible to assume variations in the ability of larval fish species in

responding to the effects of impoverished environments, and these factors should be part of the mechanisms of resilience of the community in the Pacific region. Some species in subtropical areas as the sardine in the Gulf of California modify their spawning activity and distributional range as a consequence of ENSO events (Nevárez-Martínez et al., 2001, Sánchez-Velasco et al., 2002), which can diminish the larval abundance and shift their spatial distribution. The consequences of poor spawning during the El Niño alter the recruitment to adult populations in the following years (Sánchez-Velasco et al., 2002).

The changes of the abundance of coastal fishes in the central Mexican Pacific during El Niño event (Godínez-Domínguez et al., 2000; Madrid and Sánchez, 1997) could be produced by changes in their catchability, because extreme environmental changes could modify the spatial distribution of fish populations. Apparently, pelagic species as *Katsuwonus pelamis* and the sardine *Opisthonema libertate* move towards inshore waters during warm periods searching for food (Godínez-Domínguez et al 2000). The main environmental changes in the study area during El Niño event are positive temperature anomalies and the impoverishment of primary and secondary production (Franco-Gordo et al., in review). The shortage of food could produce the displacement of fish populations and reductions in the spawning activity, and these factors could be the reason because the larval fish assemblage shows higher values of species richness, evenness and lower abundances.

One of the most cited effects of the El Niño events in zooplankton studies in the subtropical, temperate and subartic waters of the Pacific has been the tropicalization of the communities. These effects have been reported for most of the zooplanktic groups (see Franco-Gordo et al., in review), including the ichthyoplankton communities. The irruption of a warmer water mass from the south modifies the oceanographic conditions and produces a displacement of the local communities by others with more tropical affinities. So, what could we expect in tropical areas about the assemblage composition and structure?

In our case, both components of diversity, species richness and evenness, show a slight increase during El Niño event due mainly to the abundance decrease and the shift toward inshore waters of the fish community. Unfortunately there are not studies focused in the determination of changes of the larval fish diversity under El Niño events. The main effects reported in larval fish communities during warm periods are the abundance decrease and assemblage recomposition (Avalos-García et al., 2003; Smith and Moser, 2001; Funes-Rodrígues et al., 1995), but assemblage structure has not been analyzed.

The average taxonomical distinctness (AvTD) of the assemblages showed significant seasonal differences but not interannual changes. The values of the AvTD were similar in both pre- and ENSO periods,

however the lowest vales were observed during the tropical and transition seasons. According to Clarke and Warwick (2001a) low values of this statistic denote environmental stress or disturbance; the first species disappearing are predominantly representative of higher taxa that are relatively species-poor, the remaining species pertain to taxonomic groups relatively more species-rich. AvTD, together with species richness and evenness, showed the existence of a low diversity assemblage during the tropical season, which is formed by a small group of species closely related phylogenetically. Taxonomical diversity could be related with functional diversity, and in this sense AvTD index could be interpreted in this case as a functional diversity measure indicating a decrease in functional diversity of the larval assemblage during a season defined by warm and oligotrophic waters inclusive of the El Niño event.

B. bathymaster was the most important species and typify for both similarity and dissimilarity in the previous and El Niño period. Other dominant species in both periods were *D. latifrons, Gobionellus* sp., Gobidae and *V. lucetia*. The species that discriminate the El Niño period are: *H. thrissina*, *E. lineatus*, *B. panamense* and larvae of the genus *Lutjanus*. The interannual variability due to El Niño event does not implies a drastic change in the species composition of the tropical larval assemblages, and, specially, the dominant species group remains constant. The main effects are defined by a decrease of abundance and changes in the dominance patterns due to an increase in evenness. The seasonal variability of the assemblages

was similar to the interannual variability, because no changes in the dominant species group were observed, however during the tropical period (mainly during El Niño event) the similarity was most even and other species as *E. lineatus*, V. *lucetia, D. latifrons* and *Lutjanus* typified this assemblage.

During El Niño 1997-98, a drastic seasonal recomposition of the larval fish assemblages was observed in the Gulf of California (an area close to the present study area): the southern assemblage (central Gulf) was dominated by mesopelagic species as *B. panamense*, *V. lucetia* and showed a lower change than the northern assemblages which showed a more drastic seasonal recomposition of species with tropical and temperate-subartic affinity (Avalos-García et al., 2003). Typical species of the tropical Pacific as *B. panamense* and *V. lucetia* have been reported as the most frequent and dominant in the Gulf of California (Aceves-Medina et al 2002; Moser et al., 1974), however the abundance recorded during El Niño 1997-98 for *B. panamense* reached 44 to 65% of the relative abundance per cruise (Avalos-García 2003). The tropicalization of the assemblages could be determined by the ocean warming generated by El Niño, but also by the seasonal irruption of the tropical water mass in the Gulf of California.

Interannual changes could be masked by long-term shifts of some larval species. *V. lucetia* has showed a sustained increase in abundance of nearly 200-fold from the 1976-77 regime shift in the

Southern California Bight region (Smith and Moser, 2003). The seasonal and interannual expansion of the tropical community towards the north together with other decadal scale variability in the Pacific, are the main forces that determine the large-scale distributional changes of ichthyoplankton. According to Smith and Moser (2003), the effect in the middle-term of environmental variability in temperate waters could be different for demersal and pelagic fish species and they suggest that other factors outweigh the shift described above, as fishing and other environmental variability sources, making difficult to find conclusive patterns.

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Conclusiones

CONCLUSIONES

1) Se identificaron 92304 larvas de peces, que alcanzaron una densidad media de 472745 larvas·$10m^{-2}$. La composición taxonómica incluyó 132 taxa, ubicados en 19 órdenes, 60 familias, 91 géneros y 87 especies. La familia Carangidae (8 especies), Paralichthydae (7) y Cynoglossidae (6), fueron las de mayor riqueza específica. La especie mejor representada por su abundancia fue *Bregmaceros bathymaster*, que conforma el 90.43% de la abundancia total de larvas, seguida por *Dormitator latifrons* (1.9%) *Harengula thrissina* (0.85%) y Engraulidae (0.85%). Las larvas de peces capturadas en este trabajo son en su mayoría formas epipelágicas con una distribución tropical-subtropical y todas ellas han sido reportadas en las tres provincias costeras del Pacífico oriental: Oregoniana, Sandieguina y Californiana.

2) Durante el periodo ambientalmente normal, no afectado por el evento de El Niño, existe un acoplamiento biológico-ambiental que determina los patrones de estacionalidad de la producción primaria, secundaria y la abundancia de larvas de peces en el Pacífico central Mexicano, así como los patrones de su distribución espacial. Las concentraciones de biomasa zooplánctica y abundancia de larvas mostraron un comportamiento similar en términos de la distribución en el espacio y en el tiempo, ambas se comportan con marcadas temporalidades y pautas

espaciales de agregación relacionadas más con procesos físico-hidrológicos que estrictamente con factores biológicos. La distancia a la costa fue el gradiente espacial más importante como respuesta de comportamiento de los zooplánctereres a desplazamientos pasivos por movimiento de masas de agua.

3) Se distinguen tres pautas hidroclimáticas asociadas con las pautas de corrientes marinas:

(a) Periodo de la Corriente de California. Los meses con valores más altos de biomasa y abundancia de larvas de peces, fueron aquellos con valores menores de temperatura superficial del mar (enero-mayo), periodo en el cual la Corriente de California fue más fuerte y claramente influye las condiciones hidrológicas de la costa de Jalisco y Colima. La alta variabilidad de la biomasa y abundancia larval indica procesos episódicos y localizados que incrementan la productividad en las zona costera, dando como resultado una sincronía entre los ciclos de producción primaria, secundaria y abundancia de larvas lo cual ilustra el acoplamiento no sólo de procesos oceanográficos físico-químicos y los incrementos o afloramientos plánctcos, sino también de los eventos reproductivos de muchas especies de peces. La influencia de la corriente de California en el Pacífico central Mexicano caracteriza un periodo de procesos advectivos, la elevación de la biomasa zooplánctica, y una mayor abundancia de larvas.

(b) Periodo Tropical. Durante los meses de julio a noviembre un flujo cálido que fluye en paralelo a la costa hacia el norte, determina las pautas de estratificación térmica de la masa de agua costera con una termoclina profunda y bajos niveles de producción primaria, secundaria y de abundancia de larvas de peces. Durante este periodo se observó un marcado gradiente de segregación espacial de las abundancias de larvas de peces y biomasa zooplánctica en sentido perpendicular a la costa. Los mayores valores se encontraron en las proximidades a la costa. Los valores más altos de diversidad de larvas de peces coinciden durante este periodo, coincidiendo con una disminución en la abundancia de larvas y aumento en la equitatividad, aunque la riqueza específica fue menor.

(c) Periodo de transición. Los meses de junio y diciembre marcan la transición entre los periodos tropicales y de la Corriente de California.

4) El periodo El Niño se inició en la zona a partir de julio de 1997 y disminuyó hacia finales de 1998. Se manifestó principalmente por anomalías de hasta 4-5 °C que llevó a la temperatura superficial a rebasar los 30 °C, y que ocasionó un desplome en los niveles de productividad primaria, secundaria y de abundancia de larvas de peces. Las variables que mejor explican la variabilidad ambiental y los procesos de producción pelágica, son el índice de surgencias, la temperatura superficial y el índice de El Niño. Además del

empobrecimiento del hábitat pelágico, se observó una pérdida de los patrones espaciales de distribución de la biomasa zooplánctica y de la abundancia de larvas de peces, sin embargo se observó la prevalencia de los patrones estacionales a pesar de los descensos de biomasa y abundancia.

5) La variabilidad de las abundancias de fitoplancton corrobora la hipótesis a cerca de la prevalencia de los patrones estacionales normales de producción biológica estacional aún durante los eventos de El Niño, así como del fuerte acoplamiento biológico-ambiental que regula la productividad del medio marino. Durante el periodo El Niño el fitoplancton estuvo formado principalmente por pequeñas diatomeas mientras que los dinoflagelados estuvieron prácticamente ausentes. La recomposición del fitoplancton también responde a una respuesta diferenciada ante ambientes empobrecidos por la baja disponibilidad de nutrientes por efecto de El Niño.

6) Los factores más influyentes en la estructura y organización de las asociaciones de larvas de peces son la estacionalidad y el Niño. El desarreglo de los procesos costeros durante el evento El Niño propició que las pautas espaciales de distribución de las asociaciones desparecieran debido a la alteración de los mecanismos relacionados al transporte larval. Un pequeño grupo de especies dominantes formado por *Bregmaceros bathymaster, Dormitator latifrons* y *Vinciguerria lucetia* tipifica tanto el periodo

previo como El Niño y básicamente las diferencias entre periodos radican en los valores de abundancia larval. Además de las especies mencionadas la asociación que tipifica el periodo de El Niño está formada por *Bentosema panamense, Harengula thrissina, Euthynus lineatus* y especies del genero *Lutjanus*.

7) La riqueza de especies y la equitatividad fueron sensibles a la variabilidad estacional e interanual de la asociación de larvas. El uso de un indicador de distancias taxonómicas permitió encontrar uno de los rasgos más conspicuos de la asociación: durante el periodo tropical se presenta una asociación con una menor diversidad filogenético y por ende menor diversidad funcional. Al parecer un mecanismo evolutivo ha llevado a la conformación de una asociación cuyos componentes se caracterizan por una gran proximidad taxonómica y su capacidad para dominar en condiciones de bajos niveles de productividad primaria y secundaria.

Apéndice I

Tabla 1 Importancia relativa de los taxa de peces en número de organismos recolectados durante diciembre de 1995.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum.
1 *Bregmaceros bathymaster*	Brebat	3136	16353	90,48	90,48
2 *Gobionellus* sp.	Gobisp	70	375	2,02	92,50
3 *Dormitatus latifrons*	Dorlat	35	161	1,01	93,51
4 Sciaenidae	Sciaen	25	119	0,72	94,23
5 *Benthosema Panamense*	Benpan	26	118	0,75	94,98
6 *Auxis* sp.	Auxisp	16	78	0,46	95,44
7 *Vinciguerria lucetia*	Vinluc	19	75	0,55	95,99
8 *Chloroscombrus orqueta*	Chlorq	12	63	0,35	96,34
9 *Opistonema* sp.	Opissp	13	63	0,38	96,71
10 *Caranx caballus*	Carcab	12	53	0,35	97,06
11 *Syacium ovale*	Syaova	18	44	52%	97,58
12 Haemulidae	Haemul	9	41	0,26	97,84
13 *Euthynus lineatus*	Eutlin	8	40	0,23	98,07
14 *Sphyraena* sp.	Sphysp	6	30	0,17	98,24
15 Pomacentridae	Pomace	4	29	0,12	98,36
16 *Balistes polylepis*	Balpol	6	29	0,17	98,53
17 *Decapterus* sp.	Decasp	5	22	0,14	98,67
18 *Eucinostomus gracilis*	Eucgra	4	19	0,12	98,79
19 *Sphoeroides annulatus*	Sphann	3	16	0,09	98,87
20 *Abudefduf troschelli*	Abutro	3	15	0,09	98,96
21 *Harengula thrissina*	Harthr	3	14	0,09	99,05
22 *Halichoeres semicinctus*	Halsem	2	11	0,06	99,11
23 *Scorpaena* sp.	Scorsp	2	10	0,06	99,16
24 *Sphyraena ensis*	Sphens	2	10	0,06	99,22
25 *Lutjanus argentriventris*	Lutarg	2	10	0,06	99,28
26 *Symphurus atramentatus*	Symatr	2	9	0,06	99,34
27 *Caranx sexfasciatus*	Carsex	2	8	0,06	99,39
28 *Diaphus pacificus*	Diapac	2	8	0,06	99,45
29 *Albula* sp.	Albusp	1	6	0,03	99,48
30 *Symphurus* Tipo B	SymTiB	1	6	0,03	99,51
31 Engraulidae	Engrau	1	6	0,03	99,54
32 Labridae	Labrid	1	5	0,03	99,57
33 *Stegastes rectifraenun*	Sterec	1	5	0,03	99,60
34 *Halichoeres dispilus*	Haldis	1	5	0,03	99,62
35 *Serranus* sp.	Serrsp	1	5	0,03	99,65
36 *Ammodyctoides sp.*	Ammosp	1	5	0,03	99,68
37 *Mugil cephalus*	Mugcep	1	4	0,03	99,71
38 Moringuidae	Moring	1	4	0,03	99,74
39 *Bollmania* sp.	Bollsp	1	4	0,03	99,77
40 *Apogon retrosella*	Aporet	1	4	0,03	99,80
41 *Entomacrodos chiostictus*	Entchi	1	3	0,03	99,83
42 *Bathylagus wesethi*	Batwes	1	3	0,03	99,86
43 Dactiloscopidae	Dactil	1	3	0,03	99,98
44 *Paralichthys woolmani*	Parwoo	1	3	0,03	99,91
45 *Pseudograma thaumasium*	Psetha	1	3	0,03	99,94
46 *Selene brevoortii*	Selbre	1	3	0,03	99,97
47 Bramidae	Bramid	1	3	0,03	100,00

Tabla 2 Importancia relativa de los taxa de peces en número de organismos recolectados durante enero de 1996.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum.
1 *Bregmaceros bathymaster*	Brebat	4931	27201	94,39	94,39
2 *Dormitator latifrons*	Dorlat	126	286	2,41	96,8
3 *Cetengraulis mysticetus*	Cetmys	36	211	0,69	97,49
4 *Gobionellus* sp.	Gobisp	37	207	0,71	98,20
5 *Vinciguerria lucetia*	Vinluc	11	61	1,21	98,41
6 Sciaenidae	Sciaen	8	45	0,15	98,56
7 Eleotridae	Eleotr	7	38	0,13	98,70
9 *Scorpaena* sp.	Scorsp	5	28	0,10	98,79
9 *Benthosema panamense*	Benpan	5	28	0,10	98,89
10 *Halichoeres dispilus*	Haldis	5	27	0,08	98,99
11 Gobiidae Tipo A	GobTiA	4	23	0,08	99,06
12 *Psenes sio*	Psesio	4	22	0,06	99,14
13 Moringuidae	Moring	3	17	0,08	99,2
14 *Symphurus elongatus*	Symelo	4	17	0,04	99,27
15 *Eucinostomus gracilis*	Eucgra	2	16	0,06	99,31
16 *Euthinnus lineatus*	Eutlin	3	15	0,04	99,37
17 *Etropus crossotus*	Etrcro	2	12	0,04	99,41
18 *Bathycongrus macrurus*	Batmac	2	12	0,04	99,44
19 *Abudefduf troschelii*	Abutro	2	11	0,04	99,48
20 Ophidiidae	Ophidi	2	11	0,04	99,52
21 *Elops affinis*	Eloaff	2	10	0,04	99,56
22 *Synodus sechurae*	Synsec	2	10	0,04	99,60
23 *Chloroscombrus orqueta*	Chlorq	2	10	0,04	99,64
24 *Lutjanus guttatus*	Lutgut	2	10	0,04	99,67
25 *Auxis* sp.	Auxisp	2	10	0,04	99,71
26 *Syacium ovale*	Syaova	2	10	0,04	99,75
27 *Ophidion* sp.	Dionsp	1	6	0,02	99,77
28 *Lephophidium negropina*	Lepneg	1	6	0,02	99,79
29 *Pontinus* sp.	Pontsp	1	6	0,02	99,91
30 *Labrisomus multiporosus*	Labmul	1	6	0,02	99,83
31 Myctophidae	Myctop	1	6	0,02	99,85
32 *Apogon retrosella*	Aporet	1	5	0,02	99,87
33 *Xyrichtys* sp.	Xyrisp	1	5	0,02	99,89
34 *Balistes polylepis*	Balpol	1	5	0,02	99,90
35 Engraulidae	Engrau	1	5	0,02	99,92
36 *Caranx sexfasciatus*	Carsex	1	5	0,02	99,94
37 Hemiramphidae	Hemira	1	5	0,02	99,96
38 Kiposidae	Kiposi	1	5	0,02	99,98
39 *Sphyraena ensis*	Sphens	1	4	0,02	100,00

Tabla 3 Importancia relativa de los taxa de peces en número de organismos recolectados durante febrero de 1996.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum.
1 *Bregmaceros bathymaster*	Brebat	18410	93538	98,51	98,51
2 Sciaenidae	Sciaen	47	310	0,25	98,76
3 *Benthosema panamense*	Benpan	43	228	0,23	98,99
4 *Dormitator latifrons*	Dorlat	44	218	0,24	99,22
5 *Opistonema* sp.	Opissp	27	154	0,14	99,37
6 *Harengula thrissina*	Harthr	17	87	0,09	99,46
7 *Auxis* sp.	Auxisp	17	87	0,09	99,55
8 *Gobionellus* sp.	Gobisp	17	85	0,09	99,64
9 *Vinciguerria lucetia*	Vinluc	15	77	0,08	99,72
10 *Cetengraulis mysticetus*	Cetmys	12	65	0,06	99,79
11 *Symphurus atramentatus*	Symatr	3	14	0,02	99,80
12 Eleotridae	Eleotr	3	14	0,02	99,82
13 *Pontinus* sp.	Pontsp	3	13	0,02	99,83
14 *Symphurus chabanaudi*	Symcha	2	11	0,01	99,84
15 *Engyophrys sanctilaurentia*	Engsan	2	11	0,01	99,86
16 Gobiidae Tipo A	GobTiA	1	11	0,01	99,86
17 *Abudefduf troshelii*	Abutros	2	11	0,01	99,87
18 *Psenes pellucidus*	Psepel	2	11	0,01	99,88
19 *Ophidion* sp.	Ophisp	2	10	0,01	99,89
20 Moringuidae	Moring	2	10	0,01	99.90
21 *Ophichthus* sp.	Ophcsp	2	9	0,01	99,91
22 *Xyrichtys* sp.	Xyrisp	2	9	0,01	99,93
23 *Syacium ovale*	Syaova	2	8	0,01	99,94
24 *Mugil cephalus*	Mugcep	2	7	0,01	99,95
25 *Euthynnus lineatus*	Eutlin	1	6	0,01	99,95
26 *Caranx sexfasciatus*	Carsex	1	6	0,01	99,96
27 *Elops affinis*	Eloaff	1	5	0,01	99,96
28 *Synodus sechurae*	Synsec	1	5	0,01	99,97
29 *Scorpaena* sp.	Scorsp	2	5	0,01	99,98
30 *Melanostomiidae*	Melano	1	5	0,01	99,98
31 *Symphurus elongatus*	Symelo	1	4	0,01	99,99
32 *Caranx caballus*	Carcab	1	4	0,01	99,99
33 *Halichoeres dispilus*	Haldis	1	4	0,01	100,00

Tabla 4 Importancia relativa de los taxa de peces en número de organismos recolectados durante marzo de 1996.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum.
1 *Bregmaceros bathymaster*	Brebat	7182	31443	97,45	97,45
2 *Dormitator latifrons*	Dorlat	67	301	0,91	98,36
3 *Gobionellus* sp.	Gobisp	28	119	0,38	98,74
4 *Labrisomus multiporosus*	Labmul	14	67	0,19	98,93
5 *Symphurus chabanaudi*	Symcha	10	43	0,14	99,06
6 Engraulidae	Engrau	9	42	0,12	99,19
7 Sciaenidae	Sciaen	9	41	0,12	99,31
8 *Symphurus elongatus*	Symelo	9	36	0,12	99,43
9 Gobiidae Tipo A	GobTiA	8	35	0,11	99,54
10 *Bathycongrus macrurus*	Batmac	6	25	0,08	99,62
11 *Pontinus* sp.	Pontsp	5	21	0,07	99,69
12 *Cetengraulis mysticetus*	Cetmys	4	20	0,05	99,74
13 *Xyrichthys* sp.	Xyrisp	3	14	0,04	99,78
14 *Synodus sechurae*	Syncec	2	11	0,03	99,81
15 *Etropus crossotus*	Etrcro	2	10	0,03	99,84
16 *Ophidion* sp.	Dionsp	2	9	0,03	99,86
17 Gobiidae Tipo B	GobiTiB	2	8	0,03	99,89
18 *Mugil cephalus*	Mugcep	1	5	0,01	99,91
19 *Citarichthys platophrys*	Citpla	1	5	0,01	99,92
20 *Vinciguerria lucetia*	Vinluc	1	5	0,01	99,93
21 *Bhotus leopardinus*	Bholeo	1	5	0,01	99,95
22 *Ophichthus* sp.	Ophisp	1	4	0,01	99,96
23 *Symphurus atramentatus*	Symatr	1	4	0,01	99,97
24 *Syacium ovale*	Syaova	1	3	0,01	99,99
25 *Porichthys margaritatus*	Pormar	1	3	0,01	100,00

Tabla 5 Importancia relativa de los taxa de peces en número de organismos recolectados durante abril de 1996.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum.
1 *Bregmaceros bathymaster*	Brebat	5009	27269	88,87	88,67
2 Sciaenidae	Sciaen	199	1038	3,52	92,19
3 Engraulidae	Engrau	174	929	3,08	95,27
4 *Dormitator latifrons*	Dorlat	103	376	1,82	97,1
5 *Symphurus elongatus*	Symelo	57	229	1,01	98,11
6 *Harengula thrissina*	Harthr	31	168	0,55	98,65
7 *Gobionellus* sp.	Gobisp	14	51	0,25	98,9
8 Gobiidae Tipo A	GobTiA	13	49	0,23	99,13
9 *Scorpaena* sp.	Scorsp	7	44	0,12	99,26
10 Haemulidae	Haemul	5	26	0,09	99,35
11 *Eucinostomus entomelas*	Eucent	4	21	0,07	99,42
12 *Xyrichtys* sp.	Xyrisp	4	19	0,07	99,49
13 *Syacium ovale*	Syaova	3	14	0,05	99,54
14 *Paraconger nitens*	Parnit	3	12	0,05	99,59
15 *Bothus leopardinus*	Botleo	2	10	0,04	99,63
16 *Vinciguerria lucetia*	Vinluc	2	10	0,04	99,66
17 *Paralichthys woolmani*	Parwoo	2	10	0,04	99,7
18 *Symphurus chabanaudi*	Symcha	2	9	0,04	99,73
19 *Citarichthys platophrys*	Citpla	2	7	0,04	99,77
20 *Symphurus* Tipo C	SymTiC	1	6	0,02	99,79
21 *Symphurus* Tipo D	SymTiD	1	6	0,02	99,81
22 *Sphyraena ensis*	Sphens	1	5	0,02	99,82
23 *Opistonema* sp.	Opissp	1	5	0,02	99,84
24 *Ophidion* sp.	Dionsp	1	5	0,02	99,86
25 *Symphurus atramentatus*	Symatra	1	5	0,02	99,88
26 *Paraconger californiensis*	Parcal	1	5	0,02	99,89
27 *Synodus sechurae*	Synsec	1	5	0,02	99,91
28 *Cetengraulis mysticetus*	Cetmys	1	5	0,02	99,93
29 *Auxix* sp.	Auxisp	1	5	0,02	99,95
30 *Benthosema panamense*	Benpan	1	5	0,02	99,96
31 *Labrisomus multiporosus*	Labmul	1	5	0,02	99,98
32 *Chloroscombrus orqueta*	Chlorq	1	5	0,02	100,00

Tabla 6 Importancia relativa de los taxa de peces en número de organismos recolectados durante a mayo de 1996.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum.
1 *Bregmaceros bathymaster*	Brebat	12769	57805	97,41	97,41
2 *Dormitator latifrons*	Dorlat	99	450	0,76	98,17
3 Engraulidae	Engrau	70	311	0,53	98,70
4 *Harengula thrissina*	Harthr	31	140	0,24	98,94
5 *Opistonema* sp.	Opissp	22	100	0,17	99,11
6 Sciaenidae	Sciaen	21	79	0,16	99,27
7 *Vinciguerria lucetia*	Vinluc	14	71	0,11	99,38
8 *Symphurus elongatus*	Symelo	13	62	0,1	99,48
9 Gobiidae Tipo A	GobTiA	10	48	0,08	99,56
10 Labrisomidae	Labris	10	47	0,08	99,64
11 *Labrisomus multiporosus*	Labmul	7	32	0,05	99,69
12 *Gobionellus* sp.	Gobisp	5	23	0,04	99,73
13 Pomacentridae	Pomace	4	18	0,03	99,76
14 Haemulidae	Haemul	3	14	0,02	99,78
15 *Xyrichtys* sp.	Xyrisp	3	14	0,02	99,80
16 *Scorpaenodes xyris*	Scoxyr	3	13	0,02	99,82
17 *Syacium ovale*	Syaova	3	13	0,02	99,84
18 *Ophichtus* sp.	Ophisp	2	11	0,02	99,86
19 Moringuidae	Moring	2	10	0,02	99,87
20 *Sphoeroides annulatus*	Sphann	2	10	0,02	99,89
21 *Synodus sechurae*	Synsec	2	9	0,02	99,90
22 *Bathycongrus macrurus*	Batmac	1	5	0,01	99,91
23 *Eucinostomus entomelas*	Eucent	1	5	0,01	99,92
24 *Mugil cephalus*	Mugcep	1	5	0,01	99,92
25 *Etropus crossotus*	Etrcro	1	5	0,01	99,93
26 *Symphurus atramentatus*	Symatr	1	5	0,01	99,94
27 *Citharichthys platophrys*	Citpla	1	4	0,01	99,95
28 *Antherinella nepenthe*	Antnep	1	4	0,01	99,95
29 *Benthosema panamense*	Benpan	1	4	0,01	99,96
30 *Euthynnus lineatus*	Eutlin	1	4	0,01	99,97
31 Tetraodontidae	Tetrao	1	4	0,01	99,98
32 *Myrophis vafer*	Myrvaf	1	4	0,01	99,98
33 *Serranus* sp.	Serrsp	1	4	0,01	99,99
34 *Chloroscombrus orqueta*	Chlorq	1	4	0,01	100,00

Tabla 7 Importancia relativa de los taxa de peces en número de organismos recolectados durante junio de 1996.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum.
1 *Bregmaceros bathymaster*	Brebat	2860	16821	83,38	83,38
2 *Harengula thrissina*	Harthr	219	1323	6,38	89,77
3 *Vinciguerria lucetia*	Vinluc	69	404	2,01	91,78
4 *Dormitator latifrons*	Dorlat	59	350	1,72	93,5
5 Engraulidae	Engrau	39	217	1,14	94,64
6 Sciaenidae	Sciaen	36	213	1,05	95,69
7 Eleotridae	Eleotr	29	157	0,85	96,53
8 Gobiidae Tipo A	GobTiA	14	77	0,41	96,94
9 Pomacentridae	Pomace	12	64	0,35	97,29
10 *Eucinostomus entomelas*	Eucent	10	56	0,29	97,58
11 *Thalassoma* sp.	Thalsp	9	51	0,26	97,84
12 *Gobiesox* sp.	Esoxsp	7	40	0,2	98,05
13 *Symphurus chabanaudi*	Symcha	6	34	0,17	98,22
14 Gobiesosidae	Gobies	5	29	0,15	98,37
15 *Synodus sechurae*	Synsec	5	29	0,15	98,51
16 Scorpaenidae	Scorpa	4	27	0,12	98,63
17 Apogonidae	Apogon	5	27	0,15	98,78
18 *Xyrichtys* sp.	Xyrisp	4	24	0,12	98,89
19 *Syacium ovale*	Syaova	4	24	0,12	99,01
20 *Abudefduf troschelii*	Abutro	6	23	0,12	99,18
21 *Balistes polylepis*	Balpol	4	23	0,12	99,30
22 *Lutjanus guttatus*	Lutgut	4	21	0,06	99,42
23 *Gobionellus* sp.	Gobisp	2	12	0,06	99,48
24 *Auxis* sp.	Auxisp	2	11	0,06	99,53
25 *Etropus crossotus*	Etrcro	1	10	0,03	99,56
26 *Labrisomus multiporosus*	Labmul	1	6	0,03	99,59
27 *Elops affinis*	Eloaff	1	6	0,03	99,62
28 *Myrophis vafer*	Myrvaf	1	6	0,03	99,65
29 *Opisthonema* sp.	Opissp	1	6	0,03	99,68
30 *Fistularia corneta*	Fiscor	1	6	0,03	99,71
31 *Eucinostomus gracilis*	Eucgra	1	6	0,03	99,74
32 *Opistognatus* sp.	Gnatsp	1	6	0,03	99,77
33 *Lampanyctus parvicauda*	Lampar	1	6	0,03	99,80
34 *Melanocetus johnsoni*	Meljoh	1	5	0,03	99,83
35 *Chloroscombrus orqueta*	Chlorq	1	5	0,03	99,85
36 *Scorpaenodes xyris*	Scoxyr	1	5	0,03	99,58
37 *Sphyraena ensis*	Sphens	1	5	0,03	99,91
38 *Pontinus* sp.	Pontsp	1	5	0,03	99,94
39 *Cubiceps pauciradiatus*	Cubpau	1	5	0,03	99,97
40 *Lutjanus novemfasciatus*	Lutnov	1	5	0,03	100,00

Tabla 8 Importancia relativa de los taxa de peces en número de organismos recolectados durante julio de 1996.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum.
1 *Bregmaceros bathymaster*	Brebat	2279	11976	87,79	87,79
2 *Euthynnus lineatus*	Eutlin	46	241	1,77	89,56
3 Sciaenidae	Sciaen	38	185	1,46	91,02
4 *Sphoeroides annulatus*	Sphann	27	128	1,04	92,06
5 *Dormitator latifrons*	Dorlat	22	111	0,85	92,91
6 *Lutjanus novemfasciatus*	Lutnov	16	77	0,62	93,53
7 *Sphyraena ensis*	Sphens	14	64	0,54	94,07
8 Pomacentridae	Pomace	11	63	0,42	94,49
9 *Porichthys margaritatus*	Pormar	12	62	0,46	94,95
10 Eleotridae	Eleotr	12	58	0,46	95,42
11 *Vinciguerria lucetia*	Vinluc	10	55	0,39	95,8
12 Gobiidae Tipo C	GobTiC	11	54	0,42	96,22
13 Engraulidae	Engrau	10	53	0,39	96,61
14 *Benthosema panamense*	Benpan	10	50	0,39	97,00
15 *Gobionellus* sp.	Gobisp	9	43	0,35	97,34
16 *Baslistes polylepis*	Balpol	8	38	0,31	97,65
17 *Syacium ovale*	Syaova	8	36	0,31	97,96
18 Gobiidae Tipo B	GobTiB	7	34	0,27	98,23
19 *Abudefduf troschelii*	Abutro	5	25	0,19	98,42
20 Gobiidae Tipo A	GobTiA	4	21	0,15	98,57
21 *Hemiramphus saltador*	Hemsal	5	20	0,19	98,77
22 *Eucinostomus entomelas*	Eucent	4	18	0,15	98,92
23 *Symphurus chabanaudi*	Symcha	3	15	0,12	99,04
24 *Symphurus elongatus*	Symelo	3	15	0,08	99,15
25 *Caranx caballus*	Carcab	2	12	0,08	99,23
26 *Lutjanus guttatus*	Lutgut	2	10	0,08	99,31
27 Haemulidae	Haemul	2	10	0,08	99,38
28 *Etropus crossotus*	Etrcro	2	10	0,08	99,46
29 *Auxis* sp.	Auxisp	2	9	0,08	99,54
30 *Xyrichtys* sp.	Xyrisp	2	9	0,08	99,61
31 *Thalassoma* sp.	Thalsp	1	7	0,04	99,65
32 *Cubiceps pauciradiatus*	Cubpau	1	7	0,04	99,69
33 *Cheilopogon heterurus hubbsi*	Chehet	1	6	0,04	99,73
34 *Selene brevoortii*	Selbre	1	6	0,04	99,77
35 *Bathycongrus macrurus*	Batmac	1	6	0,04	99,81
36 *Opistonema* sp.	Opissp	1	5	0,04	99,85
37 *Lestidiops neles*	Lesnel	1	5	0,04	99,88
38 *Halichoeres dispilus*	Haldis	1	5	0,04	99,92
39 *Hyporhampus rosae*	Hypros	1	5	0,04	99,96
40 *Mugil cephalus*	Mugcep	1	4	0,04	99,98
41 *Anthenarius sanguineus*	Antsan	1	4	0,04	100,00

Tabla 9 Importancia relativa de los taxa de peces en número de organismos recolectados durante octubre de 1996.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum.
1 *Bregmaceros bathymaster*	Brebat	920	3789	76,67	76,67
2 *Dormitator latifrons*	Dorlat	106	416	8,83	85,5
3 Engraulidae	Engrau	33	119	2,75	88,25
4 Sciaenidae	Sciaen	24	98	2,00	90,25
5 *Euthynnus lineatus*	Eutlin	19	80	1,58	91,83
6 *Gobionellus sp.*	Gobisp	19	76	1,57	93,42
7 *Auxis* sp.	Auxisp	8	52	0,67	94,08
8 Gobiidae Tipo A	GobTiA	12	48	1,00	95,08
9 Pomacentridae	Pomace	7	33	0,58	95,67
10 *Symphyrus chabanaudi*	Symcha	6	32	0,50	96,17
11 *Benthosema panamense*	Benpan	5	26	0,42	96,58
12 *Vinciguerria lucetia*	Vinluc	1	25	0,08	96,67
13 *Cubiceps pauciradiatus*	Cubpau	5	25	0,42	97,08
14 *Xyrichtys* sp.	Xyrisp	4	18	0,33	97,42
15 *Halichoeres dispilus*	Haldis	2	18	0,17	97,58
16 *Thalassoma* sp.	Thalsp	4	14	0,33	97,92
17 *Synodus sechurae*	Synsec	3	11	0,25	98,17
18 *Eucinostomus entomelas*	Eucent	2	8	0,17	98,33
19 *Chloroscombrus orqueta*	Chlorq	2	8	0,17	98,5
20 *Lutjanus novemfasciatus*	Lutnov	2	7	0,17	98,67
21 Eleotridae	Eleotr	1	6	0,08	98,75
22 *Caranx sexfasciatus*	Carsex	1	6	0,08	98,83
23 Moringuidae	Moring	1	6	0,08	98,92
24 *Symphurus atricaudus*	Symatr	1	6	0,08	99,00
25 *Caranx caballus*	Carcab	1	6	0,08	99,08
26 *Bothus leopardinus*	Botleo	1	6	0,08	99,17
27 *Parantias colonus*	Parcol	1	5	0,08	99,25
28 Ophichthidae	Ophich	1	5	0,08	99,33
29 Priacantidae	Priaca	1	5	0,08	99,42
30 *Selene brevoortii*	Selbre	1	4	0,08	99,5
31 *Bathycongrus macrurus*	Batmac	1	4	0,08	99,58
32 *Porichthys margaritatus*	Pormar	1	4	0,08	99,67
33 *Balistes polylepis*	Balpol	1	4	0,08	99,75
34 *Sphoeroides annulatus*	Sphann	1	3	0,08	99,83
35 *Etropus crossotus*	Etrcro	1	3	0,08	99,92
36 *Abudefduf troschelii*	Abutro	1	3	0,08	100,00

Tabla 10 Importancia relativa de los taxa de peces en número de organismos recolectados durante noviembre de 1996.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum.
1 *Bregmaceros bathymaster*	Brebat	1119	4650	81,56	81,56
2 *Dormitator latifrons*	Dorlat	55	194	4,01	85,57
3 *Euthynnus lineatus*	Eutlin	37	161	2,7	88,27
4 *Syacium ovale*	Syaova	20	83	1,46	89,72
5 *Gobionellus sp.*	Gobisp	19	74	1,38	91,11
6 Gobiidae Tipo A	GobTiA	19	69	1,38	92,49
7 *Caranx sexfasciatus*	Carsex	14	57	1,02	93,51
8 *Xyrichtys* sp.	Xyrsp	13	48	0,95	94,46
9 Engraulidae	Engrau	13	46	0,95	95,41
10 *Caranx caballus*	Carcab	9	42	0,66	96,06
11 *Vinciguerria lucetia*	Vinluc	8	36	0,58	96,65
12 Sciaenidae	Sciaen	8	27	0,58	97,23
13 *Abudefduf troschelii*	Abutro	7	23	0,51	97,74
14 *Etropus crossotus*	Etrcro	3	13	0,22	97,96
15 *Cubiceps pauciradiatus*	Cubpau	3	13	0,22	98,18
16 *Hypsoblennius* sp.	Hypssp	2	10	0,15	98,32
17 *Symphurus chabanaudi*	Symcha	2	10	0,15	98,47
18 *Apogon retrosella*	Aporet	2	9	0,15	98,62
19 *Sphoeroides annulatus*	Sphann	2	9	0,15	98,76
20 *Symphurus williamsi*	Symwil	1	8	0,07	98,83
21 *Synodus sechurae*	Synsec	2	7	0,15	98,98
22 *Pomacentridae*	Pomace	2	7	0,15	99,13
23 *Ophichthus* sp.	Ophisp	1	7	0,07	99,20
24 *Auxis* sp.	Auxisp	1	6	0,07	99,27
25 *Ophidion* sp.	Dionsp	1	6	0,07	99,34
26 *Balistes polilepis*	Balpol	2	5	0,15	99,49
27 Balistidae	Balist	1	5	0,07	99,56
28 *Scorpaena* sp.	Scorsp	1	4	0,07	99,64
29 *Lutjanus argentriventris*	Lutarg	1	4	0,07	99,71
30 *Gobiesox* sp.	Esoxsp	1	4	0,07	99,78
31 *Pontinus* sp.	Pontsp	1	3	0,07	99,85
32 *Encheliophis dubis*	Encdub	1	3	0,07	99,93
33 *Scorpaenodes* sp.	Nodesp	1	2	0,07	100,00

Tabla11 Importancia relativa de los taxa de peces en número de organismos recolectados durante diciembre de 1996.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum.
1 *Bregmaceros bathymaster*	Brebat	833	4221	85,09	85,09
2 *Dormitator latifrons*	Dorlat	42	221	4,29	89,38
3 *Euthynnus lineatus*	Eutlin	24	113	2,45	91,83
4 *Vinciguerria lucetia*	Vinluc	15	88	1,53	93,36
5 *Gobionellus* sp.	Gobisp	7	33	0,72	94,08
6 *Psenes sio*	Psesio	6	32	0,61	94,69
7 *Syacium ovale*	Syaova	7	29	0,72	95,40
8 *Sphoeroides annulatus*	Sphann	3	25	0,31	95,71
9 Sciaenidae	Sciaen	5	23	0,51	96,22
10 *Auxis* sp.	Auxisp	4	19	0,41	96,63
11 *Caranx sexfasciatus*	Carsex	4	19	0,41	97,04
12 Gobiidae Tipo A	GobTiA	4	18	0,41	97,45
13 *Halichoeres dispilus*	Haldis	2	16	0,20	97,65
14 *Benthosema panamense*	Benpan	3	15	0,31	97,96
15 *Caranx caballus*	Carcab	3	13	0,31	98,26
16 *Etropus crossotus*	Etrcro	3	13	0,31	98,57
17 Pomacentridae	Pomace	3	12	0,31	98,88
18 *Symphurus chabanaudi*	Symcha	2	11	0,20	99,08
19 *Symphurus atramentatus*	Symatr	2	10	0,20	99,28
20 *Thalassoma* sp.	Thalsp	1	5	0,10	99,39
21 *Harengula thrissina*	Hartrr	1	4	0,10	99,49
22 *Trachinotus kennedyi*	Traken	1	4	0,10	99,59
23 *Chloroscombrus orqueta*	Chlorq	1	4	0,10	99,69
24 Labrisomidae	Labris	1	4	0,10	99,80
25 Moringuidae	Moring	1	4	0,10	99,90
26 *Xyrichtys* sp.	Xyrisp	1	4	0,10	100,00

Apéndice II

Tabla 1. Importancia relativa de los taxa depeces en número de organismos recolectados durante enero de 1997.

	TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1	Bregmaceros bathymaster	Brebat	1852	10407	93,60	93,60
2	Dormitator latifrons	Dorlat	66	360	3,24	96,84
3	Gobionellus sp.	Gobisp	23	131	1,18	98,02
4	Mugil cephalus	Mugcep	6	31	0,28	98,30
5	Xyrichtys sp.	Xyrisp	5	27	0,24	98,54
6	Gobiesox sp.	Esoxsp	3	19	0,17	98,71
7	Sciaenidae	Sciaen	3	16	0,14	98,86
8	Scorpaena sp.	Scorsp	2	11	0,10	98,96
9	Symphurus chabanaudi	Symcha	2	11	0,10	99,06
10	Sphyraena sp.	Sphysp	2	11	0,10	99,15
11	Chloroscombrus orqueta	Chlorq	2	11	0,10	99,25
12	Ophichthus sp.	Ophisp	2	10	0,09	99,34
13	Auxis sp.	Auxisp	2	10	0,09	99,43
14	Etropus crossotus	Etrcro	1	6	0,05	99,49
15	Opisthonema sp.	Opissp	1	6	0,05	99,54
16	Ophidion sp.	Dionsp	1	6	0,05	99,60
17	Benthosema panamense	Benpan	1	6	0,05	99,65
18	Syacium ovale	Syaova	1	5	0,04	99,69
19	Caranx sexfasciatus	Carsex	1	5	0,04	99,74
20	Scorpaenodes xyris	Scoxyr	1	5	0,04	99,78
21	Moringuidae	Moring	1	5	0,04	99,83
22	Porichthys margaritatus	Pormar	1	5	0,04	99,87
23	Vinciguerria lucetia	Vinluc	1	5	0,04	99,92
24	Psenes pellucidus	Psepel	1	5	0,04	99,96
25	Prionotus ruscarius	Prirus	1	4	0,04	100,00

Tabla 2. Importancia relativa de los taxa depeces en número de organismos recolectados durante febrero de 1997.

	TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1	Bregmaceros bathymaster	Brebat	5861	25291	97,539	97,5394
3	Dormitator latifrons	Dorlat	34	299	1,1531	98,6926
4	Gobionellus sp.	Gobisp	10	81	0,3124	99,005
5	Xyrichtys sp.	Xyrisp	11	64	0,2468	99,2518
6	Gobidae	Gobida	4	24	0,0926	99,3444
7	Symphurus chabanaudi	Symcha	5	23	0,0887	99,4331
8	Halichoeres dispilus	Haldis	2	18	0,0694	99,5025
9	Chloroscombrus orqueta	Chlorq	4	17	0,0656	99,5681
10	Cherublemma emmelas	Cheemm	3	15	0,0579	99,6259
11	Symphurus spp	Symspp	1	12	0,0463	99,6722
12	Etropus crossotus	Etrcro	1	12	0,0463	99,7185
13	Scorpaenodes xyris	Scoxyr	2	10	0,0386	99,757
14	Moringuidae	Moring	2	10	0,0386	99,7956
15	Labrisomus multiporosus	Labmul	2	10	0,0386	99,8342
16	Symphurus elongatus	Symelo	2	9	0,0347	99,8689
17	Sciaenidae	Sciaen	2	9	0,0347	99,9036
18	Tripterygiidae	Tripte	1	5	0,0193	99,9229
19	Prionotus ruscarius	Prirus	1	5	0,0193	99,9421
20	Mugil cephalus	Mugcep	1	5	0,0193	99,9614
21	Hypsoblennius brevipinnis	Hypbre	1	5	0,0193	99,9807
22	Engyophrys sanctilaurentia	Engsan	1	5	0,0193	100

Tabla 3. Importancia relativa de los taxa depeces en número de organismos recolectados durante marzo de 1997.

	TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1	Bregmaceros bathymaster	Brebat	3422	15202	96,73	96,73
2	Dormitator latifrons	Dorlat	73	307	1,95	98,68
3	Pomacentridae	Pomace	10	49	0,31	98,99
4	Mugil cephalus	Mugcep	4	26	0,17	99,16
5	Syacium ovale	Syaova	5	19	0,12	99,28
6	Halichoeres dispilus	Haldis	3	18	0,11	99,40
7	Symphurus chabanaudi	Symcha	2	14	0,09	99,48
8	Prionotus ruscarius	Prirus	4	12	0,08	99,56
9	Gobidae	Gobida	4	12	0,08	99,64
10	Xyrichtys sp.	Xyrisp	2	10	0,06	99,70
11	Gobionellus sp.	Gobisp	2	10	0,06	99,76
12	Harengula thrissina	Harthr	2	10	0,06	99,83
13	Hypsoblennius brevipinnis	Hypbre	1	7	0,04	99,87
14	Symphurus atramentatus	Symatr	1	5	0,03	99,90
15	Gobiesox sp.	Esoxsp	1	5	0,03	99,94
16	Psenes sio	Psesio	1	4	0,03	99,96
17	Scorpaenodes xyris	Scoxyr	1	4	0,03	99,99
18	Symphurus spp	Symspp	1	2	0,01	100,00

Tabla 4. Importancia relativa de los taxa depeces en número de organismos recolectados durante julio de 1997.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1 Harengula thrissina	Harthr	93	742	39,91	39,91
2 Bregmaceros bathymaster	Brebat	60	393	21,14	61,05
3 Dormitator latifrons	Dorlat	23	182	9,79	70,84
4 No identificado	Noiden	14	95	5,11	75,95
5 Lutjanus novemfasciatus	Lutnov	10	76	4,09	80,04
6 Syacium ovale	Syaova	7	44	2,37	82,41
7 Eucinostomus gracilis	Eucgra	8	44	2,37	84,78
8 Euthynnus lineatus	Eutlin	5	39	2,10	86,87
9 Balistes polilepis	Balpol	5	38	2,04	88,92
10 Vinciguerria lucetia	Vinluc	4	30	1,61	90,53
11 Gobionellus sp.	Gobisp	4	22	1,18	91,72
12 Caranx caballus	Carcab	3	21	1,13	92,85
13 Engraulidae	Engrau	3	15	0,81	93,65
14 Gobidae	Gobida	2	12	0,65	94,30
15 Sphyraena ensis	Sphens	1	10	0,54	94,84
16 Prionotus ruscaria	Prirus	1	10	0,54	95,37
17 Sciaenidae	Sciaen	1	9	0,48	95,86
18 Halichoeres dispilus	Haldis	1	9	0,48	96,34
19 Benthosema panamense	Benpan	1	8	0,43	96,77
20 Synodus sechurae	Synsec	1	8	0,43	97,20
21 Ophichthus sp.	Ophisp	1	8	0,43	97,63
22 Sphoeroides annulatus	Sphann	1	8	0,43	98,06
23 Gobiesox sp.	Esoxsp	2	7	0,38	98,44
24 Gempilidae	Gempil	2	7	0,38	98,82
25 Elops affinis	Eloaff	1	6	0,32	99,14
26 Etropus crossotus	Etrcro	1	6	0,32	99,46
27 Auxis sp.	Auxisp	1	5	0,27	99,73
28 Haemulidae	Haemul	1	5	0,27	100,00

Tabla 5. Importancia relativa de los taxa depeces en número de organismos recolectados durante agosto de 1997.

	TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1	Harengula thrissina	Harthr	163	1009	26,99	26,99
2	Bregmaceros bathymaster	Brebat	62	442	11,82	38,82
3	Euthynnus lineatus	Eutlin	63	424	11,34	50,16
4	No identificado	Noiden	67	416	11,13	61,29
5	Lutjanus novemfasciatus	Lutnov	42	250	6,69	67,98
6	Dormitator latifrons	Dorlat	39	227	6,07	74,05
7	Caranx caballus	Carcab	23	172	4,60	78,65
8	Lutjanus guttatus	Lutgut	23	127	3,40	82,05
9	Pomacentridae	Pomace	17	100	2,68	84,72
10	Vinciguerria lucetia	Vinluc	16	93	2,49	87,21
11	Benthosema panamense	Benpan	14	92	2,46	89,67
12	Eleotridae	Eleotr	15	90	2,41	92,08
13	Gobionellus sp.	Gobisp	12	71	1,90	93,98
14	Lutjanus peru	Lutper	8	31	0,83	94,81
15	Elops affinis	Eloaff	3	28	0,75	95,56
16	Sphyraena ensis	Sphens	5	22	0,59	96,15
17	Gobidae	Gobida	3	21	0,56	96,71
18	Halichoeres dispilus	Haldis	3	19	0,51	97,22
19	Auxis sp.	Auxisp	2	12	0,32	97,54
20	Xyrichtys sp.	Xyrisp	2	11	0,29	97,83
21	Gobiesox sp.	Esoxsp	1	11	0,29	98,13
22	Cubiceps pauciradiatus	Cubpau	1	11	0,29	98,42
23	Ophichthus sp.	Ophisp	1	10	0,27	98,69
24	Syacium ovale	Syaova	1	7	0,19	98,88
25	Melanocetus johnsoni	Meljoh	1	7	0,19	99,06
26	Lestidiops neles	Lesnel	1	6	0,16	99,22
27	Haemulidae	Haemul	1	6	0,16	99,38
28	Caranx sexfasciatus	Carsex	1	5	0,13	99,52
29	Sphyraena sp.	Sphens	1	5	0,13	99,65
30	Apogon guadalupensis	Apogua	1	5	0,13	99,79
31	Synodus sechurae	Synsec	1	3	0,08	99,87
32	Gnathanodon specius	Gnaspe	1	3	0,08	99,95
33	Psenes sio	Psesio	1	2	0,05	100,00

Tabla 6. Importancia relativa de los taxa depeces en número de organismos recolectados durante septiembre de 1997.

	TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1	No identificado	Noiden	48	351	20,24	20,24
2	Engraulidae	Engrau	35	242	13,96	34,20
3	Vinciguerria lucetia	Vinluc	38	239	13,78	47,98
4	Euthynnus lineatus	Eutlin	32	229	13,21	61,19
5	Lutjanus novemfasciatus	Lutnov	18	131	7,55	68,74
6	Dormitator latifrons	Dorlat	19	125	7,21	75,95
7	Benthosema panamense	Benpan	12	76	4,38	80,33
8	Bregmaceros bathymaster	Brebat	7	49	2,83	83,16
9	Gobidae	Gobida	7	48	2,77	85,93
10	Gobionellus sp.	Gobisp	7	40	2,31	88,24
11	Lutjanus guttatus	Lutgut	6	38	2,19	90,43
12	Elops affinis	Eloaff	3	26	1,50	91,93
13	Gobiesox sp.	Esoxsp	3	22	1,27	93,19
14	Auxis sp.	Auxisp	3	18	1,04	94,23
15	Labrisomus multiporosus	Labmul	2	15	0,87	95,10
16	Harengula thrissina	Harthr	2	15	0,87	95,96
17	Chloroscombrus orqueta	Chlorq	2	14	0,81	96,77
18	Selar crumenophthalmus	Selcru	2	13	0,75	97,52
19	Mugil cephalus	Mugcep	1	10	0,58	98,10
20	Syacium ovale	Syaova	1	9	0,52	98,62
21	Eleotridae	Eleotr	1	7	0,40	99,02
22	Balistes polylepis	Balpol	1	7	0,40	99,42
23	Apogon guadalupensis	Apogua	1	5	0,29	99,71
24	Myrophis vafer	Myrvaf	1	5	0,29	100,00

Tabla 7. Importancia relativa de los taxa depeces en número de organismos recolectados durante diciembre de 1997.

	TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1	Vinciguerria lucetia	Vinluc	82	480	22,72	22,72
2	Euthynnus lineatus	Eutlin	70	422	19,97	42,69
3	No identificado	Noiden	46	248	11,74	54,42
4	Dormitator latifrons	Dorlat	39	211	9,99	64,41
5	Benthosema panamense	Benpan	26	143	6,77	71,18
6	Gobidae	Gobida	23	125	5,92	77,09
7	Caranx caballus	Carcab	11	61	2,89	79,98
8	Lutjanus novemfasciatus	Lutnov	11	60	2,84	82,82
9	Engraulidae	Engrau	9	44	2,08	84,90
10	Bregmaceros bathymaster	Brebat	9	37	1,75	86,65
11	Harengula thrissina	Harthr	7	35	1,66	88,31
12	Syacium ovale	Syaova	6	35	1,66	89,97
13	Lestidiops neles	Lesnel	5	31	1,47	91,43
14	Cubiceps pauciradiatus	Cubpau	5	30	1,42	92,85
15	Lutjanus guttatus	Lutgut	5	25	1,18	94,04
16	Citharichthys sp.	Citasp	4	25	1,18	95,22
17	Albula sp.	Albusp	3	16	0,76	95,98
18	Auxis sp.	Auxisp	3	16	0,76	96,73
19	Gobionellus sp.	Gobisp	2	12	0,57	97,30
20	Fistularia corneta	Fiscor	2	11	0,52	97,82
21	Diodon holocamthus	Diohol	1	7	0,33	98,15
22	Haemulidae	Haemul	1	7	0,33	98,49
23	Sphyraena sp.	Sphysp	1	7	0,33	98,82
24	Pontinus sp.	Pontsp	1	6	0,28	99,10
25	Melanocetus johnsoni	Meljoh	1	5	0,24	99,34
26	Gobiesox sp.	Esoxsp	1	5	0,24	99,57
27	Mugil cephalus	Mugcep	1	5	0,24	99,81
28	Balistes polylepis	Balpol	1	4	0,19	100,00

Apéndice III

Tabla 1. Importancia relativa de los taxa depeces en número de organismos recolectados durante enero de 1998.

	TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1	*Bregmaceros bathymaster*	Brebat	245	1668	23,57	23,57
2	*Vinciguerria lucetia*	Vinluc	195	1243	17,56	41,13
3	*Euthynnus lineatus*	Eutlin	140	902	12,75	53,88
4	*Dormitator latifrons*	Dorlat	84	548	7,74	61,62
5	Gobiidae	Gobiid	70	472	6,67	68,29
6	Pomacentridae	Pomace	56	368	5,20	73,49
7	*Auxis* sp.	Auxisp	50	321	4,54	78,03
8	Maltratados	Maltra	47	312	4,41	82,44
9	*Benthosema panamense*	Benpan	46	301	4,25	86,69
10	*Harengula thrissina*	Harthr	30	217	3,07	89,76
11	*Syacium ovale*	Syaova	20	129	1,82	91,58
12	*Cubiceps pauciradiatus*	Cubpau	18	113	1,60	93,18
13	*Caranx caballus*	Carcab	15	100	1,41	94,59
14	*Lestidiops neles*	Lesnel	11	66	0,93	95,52
15	*Mycthophum aurolaternatum*	Mycaur	10	63	0,89	96,41
16	*Gobionellus* sp.	Gobisp	7	46	0,65	97,06
17	*Synodus Sechurae*	Synsec	5	32	0,45	97,51
18	*Lutjanus novemfasciatus*	Lutnov	5	30	0,42	97,94
19	*Bathophilus filifer*	Batfil	4	22	0,31	98,25
20	*Gobiesox* sp.	Esoxsp	3	19	0,27	98,52
21	Pontinus sp.	Pontsp	2	13	0,18	98,70
22	Labridae	Labrid	2	12	0,17	98,87
23	Cherublemma emmelas	Cheemm	2	11	0,16	99,03
24	Elops affinis	Eloaffi	2	11	0,16	99,18
25	Halichoeres dispilus	Haldis	1	8	0,11	99,29
26	Bothus leopardinus	Botleo	1	7	0,10	99,39
27	Mugil cephalus	Mugcep	1	6	0,08	99,48
28	Sphyraena ensis	Sphens	1	6	0,08	99,56
29	Scopelarchoides nicholsi	Sconic	1	6	0,08	99,65
30	Ophichthus sp.	Ophisp	1	5	0,07	99,72
31	Opistognathus sp.	Opissp	1	5	0,07	99,79
32	Scorpaenodes xyris	Scoxyr	1	5	0,07	99,86
33	Diogenichthys laternatus	Diolat	1	5	0,07	99,93
34	Halichoeres semicintus	Halsem	1	5	0,07	100,00

Tabla 2. Importancia relativa de los taxa depeces en número de organismos recolectados durante marzo de 1998.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1 Bregmaceros bathymaster	Brebat	3804	22429	91,30	91,30
2 Benthosema panamense	Benpan	147	969	3,94	95,24
3 Dormitator latifrons	Dorlat	68	408	1,66	96,90
4 Harengula thrissina	Harthr	34	197	0,80	97,70
5 Gobiidae	Gobiid	17	103	0,42	98,12
6 Vinciguerria lucetia	Vinluc	12	74	0,30	98,42
7 Psenes pellucidos	Psepel	8	47	0,19	98,62
8 Myctophum aurolaternatum	Mycaur	8	47	0,19	98,81
9 Syacium ovale	Syaova	7	37	0,15	98,96
10 Maltratados	Maltra	6	35	0,14	99,10
11 Xyrichtys sp.	Xyrisp	6	35	0,14	99,24
12 Citharichthys sp.	Cithsp	5	33	0,13	99,38
13 Gobionellus sp.	Gobisp	4	27	0,11	99,49
14 Lestidiops neles	Lesnel	4	24	0,10	99,58
15 Symphurus elongatus	Symelo	1	14	0,06	99,64
16 Symphurus chabanaudi	Symcha	2	13	0,05	99,69
17 Cubiceps pauciradiatus	Cubpau	2	11	0,04	99,74
18 Auxis sp.	Auxisp	2	11	0,04	99,78
19 Bothus leopardinus	Bholeo	2	11	0,04	99,83
20 Bathycongrus macrurus	Batmac	2	9	0,04	99,87
21 Diogenichthys laternatus	Diolat	1	6	0,02	99,89
22 Aristomias scintillas	Arisci	1	6	0,02	99,91
23 Lutjanus argentiventris	Lutarg	2	6	0,02	99,94
24 Ophidion sp.	Dionsp	1	5	0,02	99,96
25 Abudefduf troscheli	Abutro	1	5	0,02	99,98
26 Sphoeroides annulatus	Sphann	1	5	0,02	100,00

Tabla 3. Importancia relativa de los taxa depeces en número de organismos recolectados durante abril de 1998.

	TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1	Bregmaceros bathymaster	Brebat	2354	16915	91,62	91,62
2	Benthosema panamense	Benpan	47	339	1,84	93,46
3	Dormitator latifrons	Dorlat	47	331	1,79	95,25
4	Sphoeroides annulatus	Sphann	32	186	1,01	96,26
5	Syacium ovale	Syaova	21	151	0,82	97,08
6	Gobionellus sp.	Gobisp	14	92	0,50	97,57
7	Symphurus elongatus	Symelo	13	87	0,47	98,04
8	Gobiidae	Gobiid	8	55	0,30	98,34
9	Scianidae	Sciaen	6	43	0,23	98,58
10	Bathycongrus macrurus	Batmac	6	39	0,21	98,79
11	Maltratados	Maltra	5	38	0,21	98,99
12	Engraulidae	Engrau	6	37	0,20	99,19
13	Symphurus chabanaudi	Symcha	4	28	0,15	99,34
14	Xyrichthys sp.	Xyirsp	3	19	0,10	99,45
15	Synodus lucioceps	Synluc	2	17	0,09	99,54
16	Bothus leopardinus	Botleo	2	14	0,08	99,62
17	Halichoeres dispilus	Haldis	2	12	0,06	99,68
18	Scorpaenodes xyris	Scoxyr	2	12	0,06	99,75
19	Cubiceps pauciradiatus	Cubpau	1	8	0,04	99,79
20	Labridae	Labrid	1	8	0,04	99,83
21	Apogon retrosella	Aporet	1	7	0,04	99,87
22	Labrisomidae	Labris	1	6	0,03	99,90
23	Moringuidae	Moring	1	6	0,03	99,94
24	Scopelarchoides nicholsi	Sconic	1	6	0,03	99,97
25	Antennarius sanguineos	Antsan	1	6	0,03	100,00

Tabla 4. Importancia relativa de los taxa depeces en número de organismos recolectados durante mayo de 1998.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1 Bregmaceros bathymaster	Brebat	251	1670	78,59	78,59
2 Dormitator latifrons	Dorlat	22	158	7,44	86,02
3 Gobiesox sp.	Esoxsp	10	68	3,20	89,22
4 Syacium ovale	Syaova	7	43	2,02	91,25
5 Engraulidae	Engrau	6	34	1,60	92,85
6 Gobiidae	Gobiid	5	32	1,51	94,35
7 Bothus leopardinus	Bholeo	4	30	1,41	95,76
8 Lutjanus argentiventris	Lutarg	3	21	0,99	96,75
9 Vinciguerria lucetia	Vinluc	3	21	0,99	97,74
10 Bathycongrus macrurus	Batmac	1	7	0,33	98,07
11 Congridae	Congri	1	7	0,33	98,40
12 Maltratados	Maltra	1	7	0,33	98,73
13 Hypsypops rubicundus	Hyprub	1	7	0,33	99,06
14 Sciaenidae	Sciaen	1	5	0,24	99,29
15 Gobionellus sp.	Gobisp	1	5	0,24	99,53
16 Xyrichthys sp.	Xyrisp	1	5	0,24	99,76
17 Sphoeroides annulatus	Sphann	1	5	0,24	100,00

Tabla 5. Importancia relativa de los taxa depeces en número de organismos recolectados durante junio de 1998.

	TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1	Engraulidae	Engrau	117	669	38,99	38,99
2	Bregmaceros bathymaster	Brebat	71	374	21,79	60,78
3	Dormitator latifrons	Dorlat	33	193	11,25	72,03
4	Vinciguerria lucetia	Vinluc	11	66	3,85	75,87
5	Gobionellus sp.	Gobisp	11	61	3,55	79,43
6	Gobiidae	Gobiid	8	47	2,74	82,17
7	Lutjanus argentiventris	Lutarg	8	43	2,51	84,67
8	Syacium ovale	Syaova	8	42	2,45	87,12
9	Maltratados	Maltra	7	37	2,16	89,28
10	Benthosema panamense	Benpan	6	37	2,16	91,43
11	Synodus lucioceps	Synluc	5	32	1,86	93,30
12	Harengula thrissina	Harthr	7	28	1,63	94,93
13	Pomacentridae	Pomace	5	27	1,57	96,50
14	Euthynnus lineatus	Eutlin	2	10	0,58	97,09
15	Cubiceps pauciradiatus	Cubpau	1	6	0,35	97,44
16	Caranx caballus	Carcab	1	6	0,35	97,79
17	Sphoeroides annulatus	Sphann	1	6	0,35	98,14
18	Gobiesox sp.	Esoxsp	1	6	0,35	98,48
19	Paralepipidae	Parale	1	6	0,35	98,83
20	Etropus crossotus	Etrcro	1	6	0,35	99,18
21	Auxis sp.	Auxisp	1	5	0,29	99,48
22	Xyrichthys sp.	Xyrisp	1	5	0,29	99,77
23	Mugil cephalus	Mugcep	1	4	0,23	100,00

Tabla 6. Importancia relatíva de los taxa depeces en número de organismos recolectados durante julio de 1998.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1 Engraulidae	Engrau	52	330	35,91	35,91
2 Lutjanus argentiventris	Lutarg	22	125	13,60	49,51
3 Euthynnus lineatus	Eutlin	17	106	11,53	61,04
4 Gobiidae	Gobiid	9	57	6,20	67,25
5 Maltratados	Maltra	9	51	5,55	72,80
6 Vinciguerria lucetia	Vinluc	9	46	5,01	77,80
7 Caranx caballus	Carcab	6	34	3,70	81,50
8 Dormitator latifrons	Dorlat	4	28	3,05	84,55
9 Bregmaceros bathymaster	Brebat	4	27	2,94	87,49
10 Pomacentridae	Pomace	5	26	2,83	90,32
11 Abudefduf troschelli	Abutro	4	20	2,18	92,49
12 Opistognatus sp.	Opissp	2	14	1,52	94,02
13 Auxis sp.	Auxisp	2	10	1,09	95,10
14 Gobionellus sp.	Gobisp	1	8	0,87	95,97
15 Bothus leopardinus	Botleo	1	7	0,76	96,74
16 Mugil cephalus	Mugcep	1	7	0,76	97,50
17 Albula sp.	Albusp	1	7	0,76	98,26
18 Pontinus sp.	Pontsp	1	6	0,65	98,91
19 Etropus crossotus	Etrocro	1	5	0,54	99,46
20 Xyrichthys sp.	Xyrisp	1	5	0,54	100,00

Tabla 7. Importancia relativa de los taxa depeces en número de organismos recolectados durante agosto de 1998.

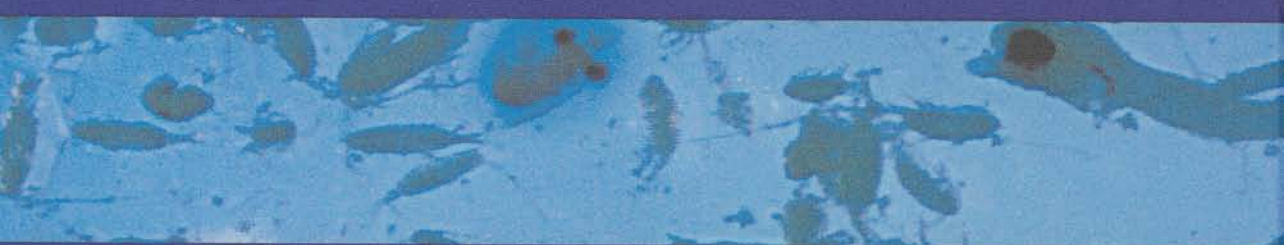
	TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1	Bregmaceros bathymaster	Brebat	83	614	30,41	30,41
2	Lutjanus argentiventris	Lutarg	65	413	20,46	50,87
3	Maltratados	Maltra	27	193	9,56	60,43
4	Gobiidae	Gobiid	17	115	5,70	66,12
5	Euthynnus lineatus	Eutlin	17	113	5,60	71,72
6	Pomacentridae	Pomace	13	81	4,01	75,73
7	Antenaridae	Anteri	11	80	3,96	79,69
8	Synodus sechurae	Synsec	8	63	3,12	82,81
9	Vinciguerria lucetia	Vinluc	8	52	2,58	85,39
10	Gobionellus sp.	Gobisp	7	42	2,08	87,47
11	Benthosema panamense	Benpan	6	38	1,88	89,35
12	Sphyraena ensis	Sphens	4	25	1,24	90,59
13	Engraulidae	Engrau	3	20	0,99	91,58
14	Halichoeres semicinctus	Halsem	2	16	0,79	92,37
15	Symphurus chabanaudi	Symcha	2	15	0,74	93,12
16	Xyrichthys sp.	Xyrisp	2	15	0,74	93,86
17	Mugil cephalus	Mugcep	2	14	0,69	94,55
18	Auxis sp.	Auxisp	2	14	0,69	95,25
19	Harengula thrissina	Harthr	2	13	0,64	95,89
20	Dormitator latifrons	Dorlat	2	13	0,64	96,53
21	Syacium ovale	Syaova	2	12	0,59	97,13
22	Gobiesox sp.	Esoxsp	2	12	0,59	97,72
23	Sphoeroides annulatus	Sphann	2	10	0,50	98,22
24	Ophichthus sp.	Ophisp	1	7	0,35	98,56
25	Lutjanus guttatus	Lutgut	1	6	0,30	98,86
26	Scorpaena sp.	Scorsp	1	6	0,30	99,16
27	Cubiceps pauciradiatus	Cubpau	1	6	0,30	99,46
28	Synodus lucioceps	Synluc	1	6	0,30	99,75
29	Etropus crossotus	Etrcro	1	5	0,25	100,00

Tabla 8. Importancia relativa de los taxa depeces en número de organismos recolectados durante septiembre de 1998.

TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1 Bregmaceros bathymaster	Bremat	1072	6019	67,37	67,37
2 Engraulidae	Engrau	190	1122	12,56	79,93
3 Dormitator latifrons	Dorlat	160	885	9,91	89,84
4 Gobionellus sp.	Gobisp	26	144	1,61	91,45
5 Benthosema panamense	Benpan	24	134	1,50	92,95
6 Gobiidae	Gobiid	21	117	1,31	94,26
7 Synodus sechurae	Synsec	13	81	0,91	95,16
8 Lutjanus argentiventris	Lutarg	13	73	0,82	95,98
9 Symphurus elongatus	Symelo	12	59	0,66	96,64
10 Harengula thrissina	Harthr	11	59	0,66	97,30
11 Maltratados	Maltra	7	31	0,35	97,65
12 Myrophis vafer	Myrvaf	4	25	0,28	97,93
13 Xyrichthys sp.	Xyrisp	3	19	0,21	98,14
14 Gobiesox sp.	Esoxsp	3	18	0,20	98,34
15 Mugil cephalus	Mugcep	3	17	0,19	98,53
16 Sciaenidae	Sciaen	3	17	0,19	98,72
17 Syacium ovale	Syaova	3	16	0,18	98,90
18 Euthynnus lineatus	Eutlin	4	14	0,16	99,06
19 Ophichthydae	Ophich	2	12	0,13	99,19
20 Symphurus chabanaudi	Symcha	2	11	0,12	99,32
21 Paraconger californiensis	Parcal	2	11	0,12	99,44
22 Sphoeroides annulatus	Sphann	2	10	0,11	99,55
23 Bathycongrus macrurus	Batmac	1	7	0,08	99,63
24 Melamphaidae	Melamp	1	6	0,07	99,70
25 Cubiceps pauciradiatus	Cubpau	1	6	0,07	99,76
26 Congridae	Congri	1	6	0,07	99,83
27 Lutjanus guttatus	Lutgut	1	6	0,07	99,90
28 Ophidion sp.	Dionsp	1	5	0,06	99,96
29 Caranx caballus	Carcab	1	4	0,04	100,00

Tabla 9. Importancia relativa de los taxa depeces en número de organismos recolectados durante diciembre de 1998.

	TAXA	CLAVE	N	Larvas m^{-2}	F(%)	F Acum
1	Bregmaceros bathymaster	Brebat	1047	6107	82,99	82,99
2	Dormitator latifrons	Dorlat	137	691	9,39	92,38
3	Gobionellus sp.	Gobisp	21	117	1,59	93,97
4	Syacium ovale	Syaova	15	89	1,21	95,18
5	Euthynnus lineatus	Eutlin	11	59	0,80	95,98
6	Benthosema panamense	Benpan	3	48	0,65	96,63
7	Engraulidae	Engrau	7	42	0,57	97,20
8	Thalassoma sp.	Thalsp	5	25	0,34	97,54
9	Caranx caballus	Carcab	3	17	0,23	97,77
10	Synodus sechurae	Synsec	3	17	0,23	98,00
11	Auxis sp.	Auxisp	2	13	0,18	98,18
12	Maltratados	Maltra	2	12	0,16	98,34
13	Caranx sexfasciatus	Carsex	2	12	0,16	98,51
14	Xyrichthys sp.	Xyrisp	2	11	0,15	98,65
15	Citharichthys sp.	Cithsp	2	11	0,15	98,80
16	Gobiidae	Gobiid	2	10	0,14	98,94
17	Moringuidae	Moring	2	10	0,14	99,08
18	Vinciguerria lucetia	Vinluc	2	10	0,14	99,21
19	Mycthophinae	Myctho	1	7	0,10	99,31
20	Cubiceps pauciradiatus	Cubpau	1	6	0,08	99,39
21	Sphoeroides annulatus	Sphann	1	5	0,07	99,46
22	Halichoeres dispilus	Haldis	1	5	0,07	99,52
23	Paralichthys californicus	Parcal	1	5	0,07	99,59
24	Congridae	Congri	1	5	0,07	99,66
25	Hemiramphus rosae	Hemros	1	5	0,07	99,73
26	Labridae	Labrid	1	5	0,07	99,80
27	Ophichthus sp.	Ophisp	1	5	0,07	99,86
28	Symphurus elongatus	Symelo	1	5	0,07	99,93
29	Pomacentridae	Pomace	1	5	0,07	100,00



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